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THE NEW SYDENHAM SOCIETY.

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THE NEW SYDENHAM SOCIETY.

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MANUAL

OF

HUMAN AND COMPARATIVE

HISTOLOGY.

EDITED BY

S. STRICKER.

ASSISTED BY

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PREFACE.

THE Translator desires to take this opportunity of thanking Dr. J. F. Payne and Dr. Broadbent for the kind aid they have given him in revising the proof-sheets of his translation of Professor Meynert's difficult essay on the Structure of the Brain in Mammals, contained in this Volume. Without their assistance, many passages that are now, he trusts, sufficiently intelligible, would have remained almost hopelessly obscure.

In the very full and careful review of the First Volume of this book, that appeared in the 121st number of the *American Journal of Medical Sciences*, attention was called to an interpolation on p. 91. It may just be stated that this was a manuscript note, forwarded by Professor Stricker with a request that it might be here inserted.

An important error occurs in Vol. I., p. 277, line 6, in the substitution of the word "former" for "latter." It should read "To the latter belong the veins," etc.

The translation of the Third Volume is nearly completed, and the first sheets are in the press.

HENRY POWER.

GREAT CUMBERLAND PLACE,
LONDON.

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OF THE PHYSIOLOGICAL INSTITUTE OF THE UNIVERSITY OF VIENNA.

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CHAPTER XVIII.

THE LIVER.

By EWALD HERING,

PROFESSOR OF PHYSIOLOGY IN THE JOSEFS-AKADEMIE IN VIENNA.

THE liver is a gland which prepares its secretion, not like other glands from arterial blood, but from the venous blood of the portal vein. The extraordinarily rich capillary plexus into which the latter breaks up, and from which the hepatic vein takes its origin, receives however also the blood of the hepatic artery after this has traversed a special capillary system serving for the nutrition of the vessels, biliary ducts, and nerves. The secreting cells of the liver are characterized by a peculiar arrangement, by virtue of which they are brought into much more intimate and extended contact with the capillaries than occurs in any other gland, whilst the number of ducts into which these cells discharge their contents is likewise much greater in comparison to the number of bloodvessels than is elsewhere seen. Considerations derived from the study of Comparative Anatomy demonstrate that the liver belongs to the group of tubular glands, although in the adult Man no tubular structure can be recognized, and only indications of its presence can be discerned in the newly born infant.

OF THE LOBULAR STRUCTURE OF THE LIVER.—The terminal branches of the arborescent and ramified hepatic veins are short, straight, or slightly sinuous vessels, which are given off at an obtuse angle from the venous trunks, or constitute their dichotomously divided extremities. They are termed *intra-*

lobular veins (*seu centrales*) because each is imbedded in the interior of one of the hepatic lobules (*lobulus seu acinus seu insula hepatis*). On each intralobular vein a small portion of the liver is seated like a raspberry on its stalk, and in correspondence with the great number of the intralobular veins, these follicles are so closely compressed that they are everywhere in immediate contact with each other, and are flattened in accordance with their mutual pressure. In the liver of certain animals, as for example in the Pig, the lobules can be easily recognized, and may even be isolated by maceration. The surface of the organ in the Pig presents to the naked eye small four, five, or six-sided areas, with a mean diameter of 1·6 millimeter. The lobules in this instance are completely separated from one another by septa of connective tissue, which, in the most superficial layer of the liver, are directed perpendicularly to the surface, and confer upon the latter the above-mentioned polygonal markings. In the liver of Man these connective-tissue septa are only very imperfectly developed, and consequently the mass of each hepatic lobule is, in him, throughout a great part of its periphery, directly continuous with the adjoining lobuli.

The portal vein, which conducts to the liver the blood collected from the abdominal viscera, gives off branches that are accompanied by those of the hepatic duct, artery, and nerves. All these structures are bound together and invested by fibrillar connective tissue, which, under the name of Glisson's Sheath (*Capsula Glissonii*), encloses also the lymphatics destined for the interior of the liver. In the liver of the Pig the angles of the elongated irregularly polyhedric lobuli are rounded off, so that where three or four lobuli impinge upon one another an interlobular canal (*canalis interlobularis*) is left between them, into which fine branches of the above-named vessels penetrate, whilst their investing connective tissue becomes directly continuous with the septa of the lobules. The course of the smaller branches of the portal vein is thus mainly determined by the form of the lobuli, since they run in the interangular spaces of the latter, *i.e.* in the interlobular spaces, and send their ultimate branches into the septa of the lobules. Hence, because the smaller branches of the portal vein only

occupy the interspaces of the lobules, and never penetrate into their interior, they are termed *interlobular* veins. And inasmuch as all the interlobular passages of the liver of the Pig contain interlobular veins, these last collectively represent the contour of the lobules; and further, as the ultimate branches of the interlobular veins are distributed in the septa, these map out the surfaces of the polyhedric lobules, and every lobule lies in a framework of portal vessels, which, however, nowhere anastomoses with the vessels of the adjoining lobule. Both those minute portal branches that lie between the adjacent angles of the lobules and those situated in the septa ultimately send numerous capillary branches into the interior of the lobules with which they are in contact, and these form a plexus traversing the entire mass of the lobules, and ultimately discharge their blood into the intralobular veins.

In the liver of Man the smaller branches of the portal vein also lie in corresponding canals between the angles of the lobuli, invested by connective tissue, though this does not form complete septa between the lobules, but sends only a few fibres between their adjoining surfaces. At the periphery of every such surface the two lobules therefore—and this indeed only partially—are separated by a little connective tissue, whilst the remainder of the periphery, and the whole of the central portion of the applied surfaces, are only theoretically present, because here the substance of the two lobules is uninterruptedly continuous. The short terminal branches of the interlobular veins lying in the interlobular spaces penetrate these incomplete septa of connective tissue, and it thus results that the angles and surfaces of the lobules in the liver of Man are similarly defined to those of the Pig by the ultimate ramifications of the portal vein which converge towards the lobuli from different quarters, without however forming any anastomosis at their periphery. From these terminal branches of the portal vein the capillary system of the lobules is then formed just as in the liver of the Pig, with this exception only, that the capillary networks of two adjoining lobules are directly continuous with each other.

If now in accordance with the above description we represent the hepatic veins as an extensively ramified tree, on the

ultimate branches of which—the intralobular veins—the hepatic lobuli are seated in the form of elongated berries, the portal vein may be regarded as a trunk penetrating the liver from the opposite side, and projecting its branches between the closely compressed lobuli as a tree forces its roots into the clefts and fissures of a rocky soil.

The surface of the liver in a living animal presents a uniform brownish-red colour, and does not give any indications of its lobular structure. In the dead animal it is also frequently quite uniform in colour in particular parts, but usually presents a more or less distinctly marbled appearance, as though it were composed of two different substances, one of a darker tint and inclined to red, the other brighter and of a yellowish hue. This is especially observable on the under surface of the liver, where the capsule is thinner, and also on the surface of sections made through the substance of the organ. The darker material sometimes forms roundish spots, whilst the brighter appears as a kind of network, in the meshes of which the dark spots are contained. In other instances, again, the darker substance forms the network, and includes brighter spots or areas. Sometimes, again, the darkly coloured portions form sinuous lines like the convolutions of the brain, the narrow interstices of which are occupied by the more brightly coloured substance. The latter corresponds to the peripheric, the former to the central portions of the lobules, and the difference in tint depends partly upon the circumstance that the peripheric portions of the lobules contain less blood than the central (Kiernan), and partly upon the biliary pigment being chiefly accumulated in the central, and the fatty substances in the peripheric portions of the lobules (Theile). The interlobular veins can frequently be recognized on the surface of the liver, even with the naked eye, as small branched or unbranched striæ or points, but the intralobular veins in the centre of the dark areas are less commonly visible. In some instances the position of each lobule is rendered evident by a slight elevation, which can be either made more conspicuous or caused to disappear by light pressure or traction.

The earlier views maintaining the existence of a completely lobular

structure in the liver were controverted by E. H. Weber,* and especially by Kiernan.† Nevertheless it is still admissible to regard the liver of Man as consisting, like that of the Pig, of lobules; for it is only on such a supposition that correct interpretations can be given of the distribution of the ultimate branches of the portal vein, as well as of the arrangement of the connective tissue.

THE STRUCTURE OF THE LOBULES OF THE LIVER.—The lobules of the liver in Man are irregularly polyhedric and usually elongated bodies about one millimeter in diameter and from one to two millimeters in length. We may distinguish in them a base, lateral surfaces, and an apex. Each lobule rests with its base on the wall of the small hepatic vein (*vena sublobularis*), from which it directly receives its internal vein. Those lobuli whose internal veins do not constitute lateral but terminal branches of the hepatic vein, coalesce completely near their bases and form a compound lobule (Theile). It frequently occurs also that an intralobular vein divides within the lobule, and that, whilst this possesses a common base, there are several apices divided from each other by more or less deep fissures.

When divided transversely, that is to say, in such a direction that the intralobular vein is struck at right angles to its course, the individual lobules of the liver present a rounded polygonal form; but when they are divided longitudinally, or parallel to the direction of the intralobular vein, they are generally elongated; and those that are compound resemble a leaf with sinuous edges, like that of the oak, or a portion of such a leaf. Wherever an intralobular vein is divided exactly at right angles, or longitudinally, it is separated from the nearest interlobular vein by an interval of about 0·5 of a millimeter, which corresponds to one half of the diameter of the lobule. The length of the capillaries extending between each intra- and interlobular vein is of course about the same. The only exception is in the case of the lobules situated immediately beneath the surface of the liver, for these are truncated above,

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* *Programmata collecta, Fasc.*, ii., Lipsius, 1851; and Müller's *Archiv Jahrgang*, 1843, p. 303.

† *The Anatomy and Physiology of the Liver, Philosoph. Transact.*, 1833.

so that their intralobular vein reaches nearer to the surface. (Kiernan).

The mass of an hepatic lobule consists essentially of two elements, the *hepatic cells* and the *capillaries*. The intralobular vein appears in the form of a short trunk that gives off in all directions branches running nearly at right angles, whilst at its upper extremity it breaks up into a brush of capillaries. The capillaries thus given off from it throughout its whole extent, dividing dichotomously, take the shortest course towards the periphery, and therefore have a predominant radial direction.

In consequence of the frequency of the dichotomous division it follows that these radial capillaries, as I may call them, are as closely arranged in the peripheral as in the central parts of the lobules; and whilst their diameter when moderately filled with injection amounts to about 0·01 of a millimeter, they are only separated by an interval of about 0·015 of a millimeter. Moreover, as the radial capillaries communicate freely with each other by short transverse anastomosing branches, a very close network is formed, with elongated meshes, the longer diameter of which has a radial direction, whilst the shorter diameter corresponds to the distance between two radial capillaries. It is only at the periphery of the lobules, where these pass without any line of demarcation into the adjoining ones, that shorter and rounder meshes make their appearance in place of the others.

Every space left between the vessels of the capillary plexus that traverses the whole lobule is filled by the hepatic cells. These constitute small soft spheroids, which, subjected to some pressure, lie between the adjoining capillaries, filling the intervening space so completely that they become mutually flattened, and are grooved by the capillaries with which they are in contact. Or we may regard the closely compressed polyhedric hepatic cells as collectively constituting a solid mass which is traversed by the numerous meshes of the capillary plexus.

From what has been stated above, it follows that in thin sections the appearances presented by the internal structure of the lobules vary considerably, in accordance with the direction in which the section is made. The radial arrangement of the capillaries, as well as the elongated form of their

meshes, is best displayed in those sections which have been made through the whole length of the intralobular vein. In such instances the lobules resemble a leaf, the midrib of which is formed by the hepatic vein. The trunk of the intralobular veins gives off capillaries on each side, which pursue a parallel course, communicating at short distances by means of transverse branches, like the lateral veins of a leaf, whilst the intralobular vein breaks up at its extremity into a group of radially directed capillaries; when the section is carried at right angles to the intralobular vein, this appears as a circular space from which the capillaries radiate outwards in all directions. It is only rarely, however, that we can follow one individual capillary through the whole of its course, because they are not given off at exactly right angles to the central trunk, but more or less obliquely. In a similar manner the meshes of the capillary plexus appear shorter than natural, because the section is not quite parallel to their plane. When the section has been carried in a direction parallel to, but not through, the long axis of the intralobular vein, a considerable number of radial capillaries will always be transversely divided, and their sections appear in or near the middle of the section of the lobule, whilst more externally they are more and more obliquely divided, until near the periphery they assume quite an irregular arrangement.

From a comparison of these simplest forms of section an interpretation may be given of the more intricate appearances presented where the section has been made at an oblique angle to the axis of the intralobular vein, whether the latter has been divided or not. In every section of the liver presenting a considerable surface, examples may be met with in which the lobules have been divided in the most various directions, because their axes really lie at all angles to one another. It must follow as a consequence of these arrangements, that the cases where the radiating capillary meshes are seen in their whole extent on one plane must be relatively rare, and it is easy therefore to fall into error respecting the arrangement of the capillaries.

Moreover the arrangement of the hepatic cells, since this is determined by that of the capillaries, varies considerably with

the direction of the section. For as we can pass from each radial capillary to several other radial capillaries, without overstepping the limits of an individual hepatic cell, we see between two such adjoining capillaries, if they lie with their whole length in the plane of the section, a single row of hepatic cells, which, on the side directed towards the axis, and on that directed towards the periphery of the lobule, is limited either by a transverse anastomosis of the radial capillaries, or becomes continuous with adjoining rows of cells. Hence the individual hepatic cells present a more or less regular cubic form, and the line of junction between two of them runs transversely from one capillary vessel to another. If the section be so thick that cells lie superjacent to the two above-mentioned capillaries, and be at the same time sufficiently transparent, the hepatic cells appear in the form of polygons with five or six sides, constituting a continuous layer, interrupted only by a few ascending and transversely divided capillaries that previously established the communication with other radial capillaries situated above the surface of section. From five to seven cells then lie around the tranverse section of such a connecting capillary. If, however, the section have struck a number of capillaries at right angles to their axes, their circular sections will be found to lie so close to each other that the adjacent ones are separated by only a single hepatic cell. Here and there short anastomosing capillaries may be seen passing from one radial vessel to another. Excluding those hepatic cells that immediately touch such anastomosing capillaries, the cells in general are in contact with two capillaries, or with one only, or rarely with three.

With these more simple structural characters we may associate a number of others, many of them exceedingly complex, which are dependent on the direction of the section, and the part through which it is carried. But the remarks already made will suffice to show that the hepatic cells will be found to be arranged in the most various manner between the capillaries; sometimes forming long rows, that at certain points coalesce into a plexiform structure, with elongated meshes, like the capillaries; sometimes forming a close network, the small round meshes of which include the transverse sections of the capillaries; sometimes resembling an epithelium composed of polygonal cells,

and sometimes so arranged as to present transitional forms to all of the above.

For the due investigation of the internal structure of the lobules, it is requisite to obtain very thin sections that shall not materially exceed the longest diameter of an hepatic cell, whilst the capillaries should be moderately distended either with blood or by means of an injection, the tint of which has not been made too deep. Considerable attention should also be paid to the process by which the hardening of the organ is effected. In alcohol, as well as in chromic acid, the hepatic cells become shrivelled, and then separate more or less completely from the neighbouring capillaries, so that a space is formed between the cells and the capillaries. The cells fall out of the capillary plexuses, and separate from one another very easily in preparations that have been hardened in chromic acid. These phenomena are by no means exclusively dependent on the concentration of the hardening fluid, nor upon the duration of its action, but rather on the condition of the liver, which, of course, varies to a very considerable extent, according to the nature of the antecedent disease, and the time after death at which the organ was first obtained and subjected to the action of the hardening fluid. In the livers of certain animals, as for example of the Rabbit, these evils are not to be feared, since not only can the organ be obtained in the perfectly fresh state, but the cells do not here easily become detached from the capillaries. The structure of the liver in the Rabbit, however, is somewhat different from the account that has been given above, the number of the capillaries in proportion to the hepatic cells being rather greater, so that each cell is in contact with three or four radial capillaries. The appearances presented by the liver in this animal, which I have elsewhere* more fully described, cannot therefore, without some restrictions, be considered as applicable to Man. The structure of the liver of the Dog is much more analogous to that of Man.

The above account of the structure of the hepatic lobules differs

* *Sitzungsberichte der Wiener Akademie der Wissenschaften*, vom. 6th Dec., 1866.

essentially from those that have been hitherto given by others. All the more recent observers, from E. H. Weber to Eberth, agree in admitting the existence of *hepatic trabeculæ*, which, composed either of one or of several rows of cells, they believe to form a plexus that interpenetrates the plexus formed by the capillaries. I have here advanced my views on the subject, because the older ones appeared to involve an impossibility, and because mine have already been corroborated by Kölliker. If the hepatic cells were really arranged in the form of trabeculæ or tubes, each mesh of the capillary network

Fig. 119.

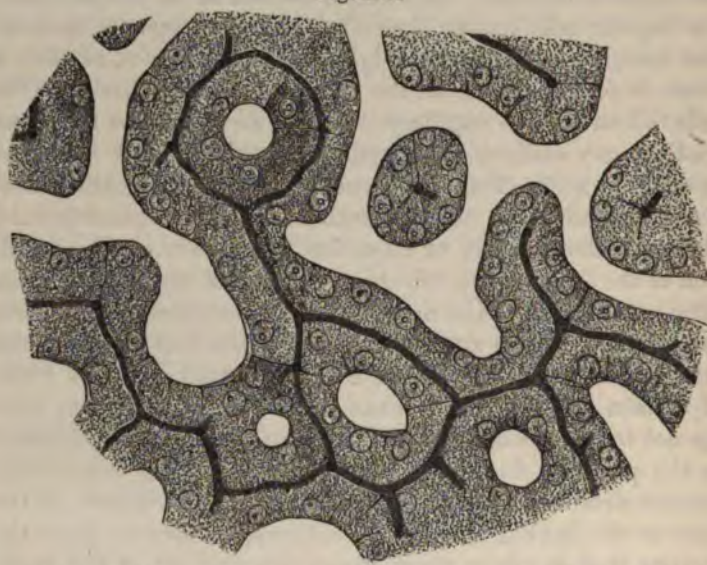

Fig. 119. From an injected liver of a Snake. In the axis of the trabeculæ, or tubular processes formed by the hepatic cells, run dark threads, which are the lines formed by the injection driven through the hepatic duct. The empty spaces between the cells correspond to the blood capillaries.

must necessarily exhibit the transverse section of one of these trabeculæ. But the rows of cells which have led to the admission of trabeculæ lie parallel to the capillaries, and to their long radially arranged meshes, and are nothing more than parts of the whole cellular mass of the liver everywhere traversed by capillaries, which have been isolated by the direction in which the section has been carried. If we could conceive numerous pallisades being planted at about the distance of their

own diameter apart, and further imagine these to be united by isolated short transverse rods, it will be obvious that, if we suppose all the intervening spaces of this trellis-work to be occupied with any kind of material, this can never assume the form of a second trabecular framework interweaving with the former, but only that of a continuous mass perforated by anastomosing canals.

I * have demonstrated, and my statements have been corroborated by the independent observations of Eberth,† in Birds, Fishes, and Amphibia, that two networks do really interpenetrate each other. In the liver of snakes, for example, the hepatic cells are arranged similarly to the epithelial cells of a tubular gland. (See fig. 119.) It is here seen that when the section exhibits the circular section of such an hepatic-cell tube, the cells appear, to the number of five or six, surrounding a small round central space, having a diameter equal to that of the biliary ducts. Both the capillaries and the gland tubes form plexuses with small round meshes, and whilst each mesh of the capillary plexus includes the section of an hepatic tube, each mesh of the plexus of hepatic tubes includes the section of a capillary. According to v. Biesiadecki,‡ the liver of Man is constructed on a similar plan, the hepatic trabeculæ exhibiting, when transversely divided, five or more cells surrounding the lumen or cavity of the passage which represents the biliary canal. I have not myself seen anything of this kind even in the liver of the new-born child, which, as contrasted with the liver of adults, does exhibit some similarity in structure to that of Amphibia—as, for example, to the Frog—inasmuch as it frequently presents three or four cells enclosed in the rounded meshes of a capillary plexus, whilst they themselves again form the parietes of a minute biliary canal.

According to the views of some few other observers, the cells of the liver in Man are arranged serially within a structureless membrana propria, forming the so-called hepatic tubules, which are united into a plexus by anastomosing branches. In these tubes a few scattered nuclei, having a diameter of 1-400 of a millimeter, may, according to E. Wagner,§

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* *Sitzungsberichte der Wiener Akademie der Wissenschaften*, vom. 11th May, 1866.

† *Medicin. Centralblatt*, vom. Dec., 1866 ; and Virchow's *Archiv*, 1867, Band xxxix., p. 70.

‡ *Sitzungsberichte der Wiener Akademie der Wissenschaften*, vom. April 4, 1867.

§ Wagner's *Archiv der Heilkunde*, 1860, *Jahrgang* i., p. 251, in which essay the whole literature of the subject is given.

be found. Beale * states that in children the tubes can be easily isolated from the capillary walls, but that in adults this can only be accomplished with difficulty, or not at all. According to the description of the structure of the lobules given above, if a membrana propria exist around the liver cells, it must also invest the capillaries, so that the membrane which I, with other observers, have considered to be merely the capillary wall, would then consist, not only of the capillary wall, but also of the membrane. Frey is of opinion that this membrane encloses the perivascular lymph space, so that the lymph is contained between it and the capillary wall.

THE CELLS OF THE LIVER.—The gland-cells of the liver of Man, discovered by Purkinje and Henle, only come under observation when they have ceased to live. If the surface of the liver exposed by section be scraped with the blade of a knife, a fluid is obtained, in which, besides other elements, numerous hepatic cells float, some of which are isolated, whilst others are united into groups. These appear as round or sometimes angular bodies, with an average diameter, according to Kölliker, of 0·018—0·026 of a millimeter, and consist of a colourless, finely granular material without any investing membrane. They contain in their interior one, or more rarely two, ellipsoidal nuclei, which, according to the same observer, have a diameter varying from 0·006 to 0·009 of a millimeter, and are sometimes discoverable with difficulty. The cell substance also frequently contains small granules or groups of granules of a yellowish or brown substance (biliary pigment), and strongly refracting molecules of various size (fat). The latter, when small, are usually numerous; but there is sometimes a single large globule invested by a thin layer of the cell substance. Such cells are frequently of unusually large dimensions.

Cells detached from hardened livers are polyhedric, and of the most varied form, often presenting pointed angular processes, whilst their edges or surfaces seen in profile are in some parts sharply defined by a dark line, and in others softened off and ragged. The cell substance is darkly granular, the nucleus very clearly defined, and often presenting a double contour.

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* *On some Points of the Anatomy of the Liver.* London, 1856.

As long as the cells of a hardened liver are *in situ*, they appear to be separated by a fine contour line, and at this point a fissure may often be discerned indicating their commencing separation. They are sometimes firmly adherent to the capillary wall, but a space usually intervenes between the two. From these appearances no conclusion can be drawn as to whether the hepatic cells possess a membrane or condensed layer investing the whole or only a part of their external surface, and whether two cells in contact are separated by a simple intervening septum, or by a cementing substance, especially since considerable differences exist in the livers of various animals. Thus, for example, the cells of the hardened liver of the Rabbit are isolated with much difficulty, and only occasionally, either from each other, or from the capillaries, whilst they do not exhibit the clefts and fissures which occur so readily in the liver of Man and many other animals.

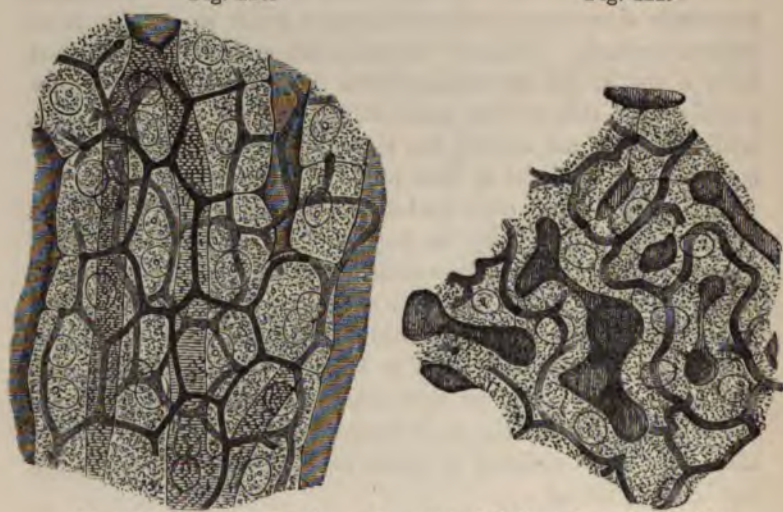
Besides the forms described above, others of a very different nature are presented by the hepatic cells; some, for example, presenting the form of discs attached to the capillaries; others being more or less fusiform, with elongated nuclei, etc., which as representing anomalous conditions will not here be further described. The hepatic cells in their living condition, being composed of a tenacious semi-fluid material, may be made artificially to assume the most varied forms, which are retained after they have stiffened in death, or have been subjected to a hardening process.

THE BILIARY CANALS OF THE HEPATIC LOBULES.—The intralobular biliary canals, or those which run within the hepatic lobules, and which are sometimes termed *biliary capillaries*, have not hitherto been described as they appear in the liver of Man, and I am compelled therefore to confine myself to the results of my own observations. The value of these chiefly depends on their coinciding with what is already known respecting the intralobular biliary canals of Mammals.

In Mammals the biliary ducts when injected (figs. 120 and 121) form a close plexus of minute and usually cylindrical canals, having a diameter of 0·001 to 0·002 of a millimeter, which runs between the hepatic cells, and forms polygonal meshes of

the same diameter as these. In certain animals, as for example the Rabbit, these canals run exclusively, and in others, as the Dog, in by far the greatest number, not along the angles, but between the planes of contact of two adjacent cells, dividing their surfaces sometimes into two equal halves, and at others unequally. Where, however, they occupy the angular space formed by the several adjacent cells, such space does not contain a blood capillary in any part of its length, nor is it in

Fig. 120. Fig. 121.



Figs. 120 and 121. Sections of an injected liver from the Rabbit. The slender biliary ducts arranged in the form of a plexus are divided longitudinally, the much wider blood capillaries transversely. The biliary ducts are also seen in section as dark points in the line representing the plane of contact (septum) between two adjoining hepatic cells. In the interior of each of the hepatic cells are one or two nuclei.

relation with a capillary at its extremities. No biliary duct therefore can be found which is not separated from a capillary by intervening cell substance. On the other hand, with rare exceptions the few angular spaces that are not occupied by a bloodvessel contain a billiary duct, and every plane surface between two adjoining cells is either traversed near its middle by a biliary duct, or is at least in contact with a duct, by one

of its borders. Wherever, consequently, in a completely injected lobule, the planes of two hepatic cells are seen in profile,—that is, as a straight line,—a biliary duct may, with few exceptions, be observed, either presenting a circular or oval section which lies in the centre of this line, or in rare cases at one of its extremities, or offering its lateral surface to the observer, and then appearing as a small rod which runs parallel to the line, and, according to the focussing of the microscope, is situated just above or beneath it.

If it be borne in mind how the hepatic cells are arranged between the capillaries, it becomes evident that when in fine sections only a single series of cells is visible between two radial capillaries, the biliary ducts must appear partly in section within the transverse lines which, as profile views of the line of junction of two cells, run from one capillary to the other, and must partly present their lateral aspect more or less foreshortened as canals that are approximatively parallel to the capillaries, and intervene between them. But if in these sections the hepatic cells appear in the form of an epithelium then the biliary ducts will constitute a plexus with polygonal meshes, each of which includes an hepatic cell (fig. 120). Again, if in thin sections the radially arranged capillaries are seen to be transversely divided, the biliary ducts will be partly seen in transverse section, and for the most part within the lines which, as profile views of the line of junction of two cells, unite two capillaries together; or more rarely they will form points where the surfaces of several cells are applied to each other; and finally in part in the form of a plexus, each mesh of which is occupied by a capillary vessel (fig. 121).

The above description has been drawn up from the appearances presented by injected preparations. The liver of Man, which at the earliest can only be investigated some hours after death, has by that time become so altered from incipient coagulation of the hepatic cells that the biliary canals of the lobules can no longer be injected. Nevertheless they are still accessible, even without injection, to observation, and with very high powers it will then be found that their arrangement is precisely similar to that of other Mammals. After I had given a detailed description of the biliary ducts of the liver of the

Rabbit, it was thought that the same account would be also applicable to that of Man, with which, however, subsequent experience has shown that it does not completely correspond. The structure of the human liver accords much more closely with that of the Dog, to the points of difference between which and that of the Rabbit reference has already been made. In the liver of Man by far the greater number of interlobular biliary ducts undoubtedly run between the adjacent planes of the hepatic cells. Still ducts are also found occupying the angles where three, or in very exceptional instances four, cells are in apposition, which is rarely found to occur in the liver of the Rabbit. This feature constitutes the essential difference between the structure of the liver in Man and the Rabbit.

If very fine sections of the hardened liver of Man be examined, a small fissure-like opening will under favourable circumstances be found in the middle of the contour lines of two adjoining cells. The line divides near its centre into two branches, which immediately coalesce again, and thus enclose the opening. Sometimes the opening presents an oval or circular form. It may frequently be shown by an alteration in the focussing that this opening is the transverse section of a canal; for the contour of the tube may be traced for some distance, foreshortened as it recedes from the eye of the observer. Again, round or more frequently triangular spaces may be observed at the angle where three adjoining cells meet. It is however impossible to decide in regard to the latter, whether they do not perhaps correspond only to fissures which have formed at the angles of the cells in consequence of the extraordinary facility with which these separate from one another. In fig. 122 such biliary passages are seen in transverse section, sketched from the liver of an infant. In very young children they can be demonstrated with great facility.

In many human livers the lobular biliary ducts can be followed with as much accuracy and as completely as in the best injected livers of animals. It especially occurs that the finely granular yellow colouring matter of the hepatic cells is exclusively deposited in the immediate vicinity of the biliary ducts, whilst the remainder of the liver is free. Every transverse section of a biliary duct is in such cases surrounded by a yellow area,

giving the impression that the cell substance adjoining the biliary ducts has become stained with bile. In similar cases it may be shown that by far the greater number of the biliary ducts run between the planes of junction of adjoining cells, and but seldom along the borders. It is observable that when the

Fig. 122.

Fig. 122. From the liver of a child three months old, hardened in chromic acid. The hepatic cells with their single nuclei are separated from the capillary wall by a small intervening space. The capillaries contain closely compressed coloured, and a few colourless, blood corpuscles. A few elongated nuclei belonging to the capillary wall are seen. Within the line of junction (septum) between two hepatic cells the transverse section of a biliary duct is seen as a small transparent space. There is also one at the angle where several of these cells come into contact.

hepatic cells are arranged like an epithelium, the biliary ducts present the form of a plexus with five or six-angled meshes, each of which includes an hepatic cell; in short, the appearances found are precisely similar to those which have been above described as occurring in the liver of Mammals.

As I have elsewhere shown in regard to the intralobular

biliary passages of the liver in Rabbits, those also of Man do not possess a membrana propria lined by hepatic cells, but are immediately bounded by these cells themselves; and the limiting wall of the biliary duct, in the event of its isolation being in any case accomplished, may be considered to be a condensed surface layer of the cell substance, or a cell-membrane, or a cuticula, which all amount to the same thing.

The injection of the intralobular biliary passages is easily accomplished in rabbits by throwing a solution of Prussian-blue in water into the ductus choledochus, under a pressure of 20—30 millimeters of mercury (Mac Gillavry), especially if the precaution be adopted of bleeding the animal to death, and rendering the liver anæmic by opening the inferior vena cava. In other animals I have not hitherto succeeded in injecting the whole of a lobule. The method suggested by Chrzonszczewsky * is well adapted for the livers of animals which are difficult to inject. It consists in the repeated injection of indigo-carmine into the blood of the living animal; after which the biliary ducts are found to be filled with the colouring matter.

The key to the right understanding of the course of the intralobular biliary passages lies in the fact that they do not, as a general rule, run along the borders, but between the planes of the hepatic cells; and inasmuch as my statements on this point have been already corroborated by Kölliker,† and in part also by Eberth,‡ I have made them the basis of the foregoing account. The intralobular biliary passages were first incompletely injected by Gerlach § in the liver of the Pig, and first completely injected by Budge || in the liver of the Sheep. The latter, however, did not represent them as intercellular passages, but as tubes provided with a nucleated membrana propria, invested externally by the hepatic cells. MacGillavry coincided with

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* Virchow's *Archiv*, 1866, Band xxxv., p. 153.

† *Handbuch der Gewebelehre*, 5th Edition, 1867.

‡ *Loc. cit.*, and in Schültze's *Archiv für Mikroskopische Anatomie*, Band iii., p. 432.

§ *Gewebelehre*, 2nd Edition, 1854, p. 332.

|| Reichert und Du Bois Reymond's *Archiv für Anatomie und Physiologie, Jahrgang*, 1859, p. 642.

this view, with the exception of the nuclei, describing the intralobular ducts as a "capillary plexus" with proper walls, in relation to which the plexus of blood capillaries was so disposed that it became "a matter of accident whether the two systems of tubes were in contact with one another, were interwoven, or altogether independent of each other." Chrzonszczewsky, Frey, and Irminger also adopted this view. On the other hand, according to Andrejevic,* the intralobular passages in the Rabbit "are visible at the borders and their points of junction at the angles of the hepatic cells," so that "their position correspond exactly to that of the intercellular passages of vegetable parenchyma." Eberth, indeed, corroborated my statement that the biliary passages ran along the surfaces of the hepatic cells; but he explained the entire structure of the mammalian liver quite differently from myself. According to him, in the incompletely injected liver of Mammals, "the anastomosing trabeculæ of the hepatic cells exhibit ducts lying in their axes, intercommunicating with one another without any, or with only incompletely filled, lateral branches." The distance between the axial biliary passages coursing along the borders of the cells of the trabeculæ and the bloodvessels amounts to the diameter of an hepatic cell, and the "lateral branches may either run along the borders of several contiguous cells, or between the surfaces of two opposed cells," and in part terminate by blind extremities. He gives two illustrations corresponding to this description from the liver of the Rabbit. To my idea, however, neither the description nor the illustrations tally with the characters presented either by the liver of Rabbits or of the Amphibia. I have only been able to discover something similar to it in the new-born child. I have never been able to discover blind extremities to the biliary passages in the completely injected hepatic lobules of the Rabbit. Biesiadecki describes the intralobular biliary ducts of Man in the same terms as Eberth, except that he considers that, as a general rule, they run in the axis of the hepatic trabeculæ, which, as already said, usually present, on transverse section, five cells surrounding the biliary duct.

In biliary passages injected with a mixture of gum and nitrate of silver, Eberth saw a delicate doubly-contoured membrane, to which he has given the name of membrana propria,—a term usually employed to designate a membrane investing the glandular epithelium externally, but not a cuticular formation, such, for example, as is exhibited by the columnar epithelium of the intestinal canal. I have personally

* *Sitzungsberichte der Wiener Akad. der Wissenschaften*, for 1851, Band xliii., Abtheil 1.

only opposed the existence of a membrane analogous to the wall of the blood capillaries, such as was supposed to be present by the above-named inquirers, but have not expressed any opinion against a wall composed of the cell membranes, although in opposition to MacGillavry and Chrzonszczewsky I have been as unsuccessful as Eberth in isolating it.

The most recent description given by Kölliker agrees in all essential points with my statements, and he has correctly added that, under certain circumstances, the transverse sections of the intralobular biliary passages can even be seen in the uninjected liver of the Rabbit, and has expressed the hope that at some future time the passages of the human subject may be similarly seen.

THE BILIARY DUCTS.—The principal divisions of the common biliary duct occur coincidently with and accompany those of the portal vein and hepatic artery, and hence sections of the biliary ducts are constantly met with in the vicinity of transverse sections of the portal vein. From these principal branches the finest ducts situated between the lobules take their origin. There is still a secondary mode of division, characterized, like that of the hepatic artery, by the anastomosis of the branches. Even before the common duct and its principal divisions enter the substance of the liver, superficial branches are given off, which subdivide, and anastomose in the connective tissue occupying the fissures of the liver. This plexus is continuous with others that run in Glisson's sheath, surrounding the larger branches of the portal vein and biliary duct, and receive their rootlets from the latter. Branches from all these plexuses penetrate, as Beale and Henle have shown, into the parenchyma of the liver, and finally give off the interlobular ducts. Moreover, at various points of the liver, biliary ducts are distributed upon its surface, which branch in the adjoining connective tissue, and form anastomoses. The isolated biliary ducts of the left lateral ligament, which extend even to the diaphragm, are derived from this source. The biliary ducts, down to those of 0·25 of a millimeter in diameter, are beset with small simple or compound glands, which, according to Riess* and Kölliker, are imbedded in the

* Reichert und Du Bois Reymond's *Archiv*, 1863, p. 473.

wall of the duct. These consist of round or elongated, often cæcum-like processes, having a diameter of 0·035—0·045 of a millimeter, which either open directly into a biliary duct, or coalesce in small numbers to form a canal, which again may either open separately into the duct, or may join with others to form a common excretory duct, and then resemble an acinous gland. This excretory duct sometimes runs for a short distance in the wall of the biliary duct, before opening into it.

The wall of the trunk and larger branches of the biliary duct can be shown to consist of an internal layer of mucous membrane and an external fibrous sheath. The latter contains smooth muscular fibres (Henle) and a few bloodvessels, whilst the former is lined by a single layer of tall columnar cells, and supports a very close capillary plexus. The medium-sized biliary ducts have a columnar epithelial layer, the cells of which are not so high, and a wall composed of a single layer, that, according to Heidenhain,* also contains contractile fibre-cells. The finest ducts, lastly, are characterized by only possessing an epithelial layer, which seems to lie free in the interlobular connective tissue, and consists of polyhedric cells, elongated in the direction of the axis of the tube. The cuticula, consisting of the transparent basement membrane of the columnar epithelium lining the larger ducts, becoming attenuated, is continued on the flatter cells of the finer ducts, and confers upon their lumen a remarkably sharp outline (Eberth). The form of the nuclei of the epithelial cells accords with the form of the latter; being long-oval in the columnar cells of the coarser, round in the more flattened cells of the medium-sized, and oval in the cells that are somewhat elongated in the direction of the axis of the tube, and which line the smallest biliary ducts.

The free surface of the mucous membrane of the common hepatic duct exhibits numerous shallow, irregularly arranged depressions. Similar depressions are found in the several branches of the duct, down to those which do not exceed 0·5 of a millimeter in diameter, the only difference being that they

* *Studien des Physiologischen Instituts zu Breslau*, Heft iv., p. 241.

are here arranged in two opposite longitudinal rows. These correspond to the openings of the lateral branches of the duct, or in other words to the larger excretory ducts of the gland. Minute punctiform pores in or between the fossæ lead into the glands of the biliary ducts.

The epithelium lining the glands of the hepatic ducts does not present any peculiarity, but like that of the ducts into which the glands open, is columnar; and they may therefore be regarded as eversions of the internal surface of the ducts, especially since, in ducts of 0·2 millimeter in diameter, they appear in the form of small and ultimately very slightly raised projections.

The smallest biliary ducts, arriving from different quarters at the same hepatic lobule, do not anastomose with one another;

Fig. 123.

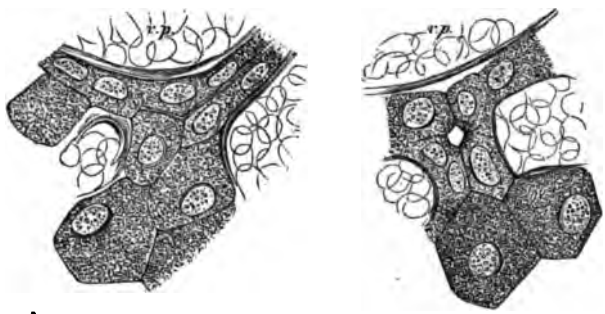

Fig. 123. Preparations made from the liver of a child three months old, hardened in chromic acid. Both figures represent fragments of a section carried through the periphery of a lobule. The coloured corpuscles of the blood are recognized by their circular contour; *v p* corresponds to an interlobular vein, in immediate proximity with which are the epithelial cells of the biliary ducts, to which, at the lower part of the figures, the much larger hepatic cells suddenly succeed.

but those which accompany a particular interlobular vein appear, in some instances, to do so around it, though this is a point that requires further investigation. These ducts pass, without material diminution of their calibre, into the intralobular biliary canals or capillaries. The hepatic cells make

their appearance suddenly, succeeding to the ultimate epithelial cells of the ducts, and it is only occasionally that these appear somewhat enlarged at the point of transition. The interior of a biliary duct is frequently bounded on the one side by small epithelial cells, whilst on the other the large hepatic cells are visible. In fig. 123 two fragments are depicted from the periphery of an hepatic lobule, taken from a child three months old, exhibiting the transition of the epithelial into the hepatic cells. Very similar appearances may be obtained from the injected livers of animals, where the fine threads of injection proceeding from the ducts, lined with epithelium, can be seen to penetrate between the hepatic cells.

It is to the absence of intermediate or transitional forms of cells between the small epithelium and the large hepatic cells, that the obscurity which has so long rested on the passage of the biliary ducts into the biliary canals is mainly to be attributed. This transition, in fact, only consists in the sudden alteration in the form of the biliary ducts, whilst the calibre of the tube undergoes but little change.

The microscopic appearances of the biliary ducts and their epithelial lining are easily observed in thin sections. In order to render the mode of branching of the biliary ducts and the plexuses visible, they should be injected with coloured material, which however, of course, destroys the epithelium. The glands of the biliary ducts are best examined microscopically after they have been injected with slightly tinted gum.

THE GALL-BLADDER is lined by a mucous membrane which presents numerous decussating rugæ and a few less elevated conical processes. Like the mucous membrane of the intestine and the villi, it is highly vascular, and is covered by a layer of very tall columnar cells, which, like those of the small intestine, present a thickened striated hem or border at their free extremity.* A layer, composed of connective tissue, traversed by a wide-meshed plexus of capillaries, and containing numerous decussating bundles of smooth muscular fibres, is regarded by Henle as belonging to the mucous membrane.

* Virchow, Virchow's *Archiv*, 1857, Band xi., p. 574.

It is invested externally by another layer of connective tissue, and where the surface of the gall-bladder is exposed this is again covered by the peritoneum. The bloodvessels, and especially the veins of the gall-bladder, are both numerous and large. The arteries, according to Beale, are each accompanied by two veins that frequently communicate by short branches passing over or under the artery, so that the whole venous system closely resembles the usual arrangement of the lymphatics.

Numerous large subserous lymphatics are distributed on the free surface of the bladder; but minute lymphatic vessels have not been demonstrated, either in this part or between the several layers of which it is composed. According to Luschka,* the parietes of the gall-bladder contain small isolated mucous glands, like those of the cystic and hepatic ducts, and the ductus communis choledochus. From a consideration of its structure, the cystic duct must be regarded as a prolongation of the gall-bladder.

E. H. Weber described the plexiform and anastomosing biliary ducts situated in the transverse fissure under the term vasa aberrantia, because he considered them to be ducts, the parenchyma belonging to which had not been developed. He took a similar view of the nature of other ducts that may be found lying externally to the proper substance of the liver. Theile,† on the other hand, in consequence of his discovery of the glands of the biliary ducts, regarded all these ducts of the transverse fissure as plexiform anastomosing mucous glands, as well as that plexus of biliary ducts he found in the capsule of Glisson. But he considered the ducts found in the ligamentum triangulare sinistrum (Ferrein, Kiernan), those found in the connective tissue that sometimes forms a bridge over the inferior vena cava between the right lobe and the lobulus Spigelii (Kiernan, Theile), those in the fossa for the umbilical vein (Kiernan, Weber), and those at the sides of the gall-bladder, to be biliary ducts, which have lost their proper lobular substance by atrophy. That this is correct in regard to a portion of these ducts, at least, may be concluded from the circumstance that in old people the sharp edge

* Henle and Pfeuffer's *Zeitschrift für Rationelle Medicin.*, 1858, Band iv., p. 189.

† Rud. Wagner's *Handwörterbuch der Physiologie*, Band ii., 1844.

of the liver undergoes metamorphosis by atrophy into a mass of connective tissue, and a similar condition is exhibited by the so-called tight-lace liver, where the pressure of the belt has produced a callous furrow on the surface of the liver.

Subsequently, Wedl,* Beale, and more recently and very fully, Henle† and Riess, have described the mucous glands and the plexuses of the biliary ducts, the last-named author particularly insisting upon the circumstance, that on account of the glands being imbedded in the walls of the ducts, they cannot be regarded "as appendices of the ducts as a whole, but only as appendices of their lumen."

THE BLOODVESSELS OF THE LIVER.—The liver contains two systems of capillary bloodvessels in its substance, belonging respectively to the portal vein and the hepatic artery. The former, which has been already described, usually exhibits large capillaries and small meshes; the latter, small capillaries and large meshes; the former is distributed throughout the interior of the lobules; the latter is limited to their external surface. Both are so far continuous with one another, that the blood traversing the capillary system of the hepatic artery enters, partly directly, and in part indirectly, into the capillary system derived from the portal vein, so that ultimately the intralobular veins carry off the blood which has traversed both the portal vein and the hepatic artery.

Both of these vessels ramify quite independently of the hepatic vein; the branches of the portal vein are invested by the loose connective tissue of Glisson's sheath, whilst the hepatic veins are firmly adherent to the substance of the liver, only a small quantity of connective tissue being interposed. The inter- and intralobular veins originate in part from the terminal branches of small portal or hepatic venous branches, but partly also as lateral branches of the larger trunks. The larger branches of the portal and hepatic veins do not, however, give off any inter- or intralobular veins to the lobules that immediately surround them. The latter, therefore, must

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* *Sitzungsberichte der Kaiserliche Akademie der Wissenschaften zu Wien*, 12th Dec., 1850, Band v., p. 481.

† *Handbuch der Anatomie*, Band ii. *Eingeweidelehre*, 1866.

receive their supply of both sets of vessels by a circuitous route. The hepatic vein also differs from the portal in giving off such direct intralobular branches into the adjoining lobules from relatively larger trunks. As a consequence of this, fine pores can be distinguished near the larger openings on the internal surface of the hepatic vein, which lead into the intralobular veins. The small hepatic veins (*venæ sublobulares*) which give off the intralobular veins on every side, apply themselves to the bases of the surrounding lobules; only isolated lobules are seated on the large veins; elsewhere they present their sides or apices to these veins.

The branches of the portal vein never anastomose with one another; and even where two interlobular veins, coming from opposite quarters, run between the same lobules, they do not communicate, but break up into capillaries. In like manner no anastomoses occur between the branches of the hepatic vein; and lastly, the portal and hepatic veins communicate in no other way than through their capillaries.

The hepatic artery exhibits a remarkable peculiarity, which has an important bearing on the mechanics of the circulation in this organ; namely, that its branches anastomose with each other, and form a wide-meshed plexus, that partly surrounds the structures lying in Glisson's sheath (*rami vasculares arteriosi*), and the large veins, and are partly distributed in the capsule (*rami capsulares arteriosi*). From this arterial plexus capillaries arise which are very narrow in comparison with the capillaries of the portal vein, and, where they do not form the close capillary plexus belonging to the larger biliary ducts, run in wide loops, and form very wide plexuses. These capillaries accompany the larger vessels, penetrate with Glisson's sheath between the lobules, and are also distributed in the capsule of the liver. The blood they transmit is collected in part, as was first shown by Ferrein, into small veins which, constituting the so-called internal rootlets of the portal vein, accompany in pairs each arterial branch (Beale), and open into branches of the portal vein, whilst a part is discharged directly into the portal capillaries; the latter taking place where both capillary plexuses lie in close proximity, as in the capsule and in the interlobular connective tissue; the former, where thick layers

of connective tissue divide the two systems of capillaries, as on the larger blood- and biliary-vessels.

Small branches of the portal vein and hepatic arteries commonly travel to the capsule through the intermediate passages of the most superficial lobules. The former quickly break up into their terminal branches, and are comparable to the interlobular veins, supplying the lobules with blood on the surface covered by the capsule. The latter having reached the capsule, immediately divide, frequently in a stellate manner, the branches sometimes forming loops which join with others to constitute a wide-meshed arterial plexus, which anastomoses with the mammary, phrenic, and suprarenal arteries.

The capillary plexus of the lobules can be injected either from the portal vein, the hepatic vein, or the hepatic artery; but the capillaries of the hepatic artery can only be filled by injections introduced through the artery itself.

Theile has given a very accurate account of the bloodvessels of the liver, describing the arterial plexus in Glisson's sheath and in the capsule as the plexus arteriosus. I do not however find he mentions that the larger hepatic veins are surrounded by an arterial plexus. Joh. Müller believed that the blood passed directly from minute arterial interlobular branches into the capillary plexus of the portal vein; but Theile found that these also broke up into capillaries like the arterial branches accompanying the interlobular veins, as can be readily shown in the liver of the Pig. Theile, Henle, and Kölliker agree with Joh. Müller in admitting the existence of peculiar rami venosi capsulares, which, forming the above-mentioned internal roots of the portal vein, convey the blood from the arterial capillaries of the capsule into the branches of the vena portæ.

THE LYMPHATICS OF THE LIVER.—The liver in Man is richly supplied with lymphatics, which here, as elsewhere, are associated with the connective tissue, and do not essentially differ from those of other organs. The capillaries, as well as the larger vessels, form frequent anastomoses. Numerous trunks, provided with valves, carry off the lymph, in part through the great fissure of the organ, and partly through the capsule, where, especially near the ligamentum suspensorium, they are very abundant.

The *superficial lymphatics, i.e.*, those distributed in the capsule, with their capillaries and smaller trunks, form an extremely close plexus, the meshes of which are much closer than those of the arterial plexus in the same situation. The two plexuses are quite independent of each other. The larger trunks accompany the capsular arteries, usually in pairs, which communicate by numerous transverse branches passing over or under the artery.

The *deep lymphatics, i.e.*, those situated in the sheath of Glisson, are also very numerous, and anastomosing frequently form a plexus, the meshes of which are not quite so close as those of the capsule. In a transverse section, which had divided a portal vein of 0·8 millimeter in diameter, I counted the sections of twenty lymphatics surrounding it. At the surface of the liver the deep and superficial lymphatics anastomose, and numerous trunks run up to the capsule with the capsular arteries of the hepatic arteries and small branches of the portal vein.

It is comparatively easy to demonstrate the microscopic lymphatics of the liver in Man. They may be shown by merely plunging the injection pipe into the connective tissue, or by injecting the biliary ducts, from which, if the force applied be somewhat too great, the fluid readily escapes, when they become filled with a coloured fluid. These methods, however, which are dependent on chance for their success, often give imperfect and unsatisfactory results. The injection of the lymphatic trunks as practised by Teichmann furnishes much more certain and trustworthy preparations. In this mode a minute opening is made with a needle into as fine a capsular lymphatic as possible, and a small canula is introduced in such a manner that when the injection is driven in it pursues the same direction as the lymph during life. As soon as one or several large trunks have been completely filled they are compressed, and the obstructed fluid now runs backward into the small peripheric vessels which have only incomplete valves. The numerous anastomoses of the lymphatics permit in this way the injection of considerable tracts both of the superficial and of the internal lymphatic systems to be effected. I do not tie the slender conically formed canula into the vessel, but hold

it firmly in the hand for the short period that the injection is entering, as this forms a sufficient obstruction to the escape of the fluid; no strong or persistent pressure must be applied if it be desired to obtain trustworthy preparations. All other methods are far less satisfactory in their results.

The illustrations of the lymphatics of the liver published by Teichmann are so far imperfect that the various parts of the plexuses are very unequally injected, and the vessels consequently everywhere presented a knotted appearance. When well injected with a semi-fluid injection, with moderate pressure, the lymphatics especially of the capsule present remarkable regularity of form.

Kölliker observed that in various animals the hepatic veins were also surrounded by lymphatics, an arrangement which has not been observed to occur in Man. According to Mac Gillavry, the deep lymphatics of the liver of the Dog are in direct communication with fissures in the connective tissue of the capsule of Glisson, that possess no proper walls. This observer injected a watery so gummy solution of Prussian blue against the valves in the large lymphatics of the portal vein, or simply plunged the instrument into the connective tissue. In either case considerable pressure was required to propel the injection, both on account of the great extent of the lymphatic system and the frequent occurrence of extravasations. But since it is only by the detection of the characteristic epithelial markings that it is possible to distinguish between a lymphatic vessel, whose form has been altered by the employment of too great force in driving the injection, and a fissure in the connective tissue caused by extravasation, I do not myself, however, place much reliance on Mac Gillavry's observations. And moreover the results of my injections of the lymphatics of the liver in Man, performed as above described, are opposed to his observations.

According to Biesiadecki, the entire capillary system of the lobules in Man floats in lymphatic spaces, the form and arrangement of which are precisely similar to the capillaries themselves, except that they are wider, and consequently contain the capillaries in their interior. On this view the hepatic cells and the capillaries must everywhere be separated by a space filled with lymph. These so-called *perivascular lymphatic spaces* were originally described by Mac Gillavry* in the liver of the Dog, and subsequently by Frey and Irminger† in the liver of the

* *Sitzungsberichte der Wiener Akademie der Wissenschaften*, April, 1864.

† *Zeitschrift für wissenschaftliche Zoologie*, 1860, Band xvi., p. 208.

Rabbit, and other Mammals. According to a provisional communication by Kisselew,* these perivascular lymphatic spaces in the liver of the Dog and Pig possess an epithelium identical with that lining the true lymphatics, and may consequently be regarded as perivascular lymphatic vessels. All the observers just mentioned agree in stating that these intralobular lymphatics freely communicate with the interlobular lymphatics situated in the connective tissue of Glisson's capsule.

I am of opinion that the existence of such perivascular lymphatic vessels has not hitherto been satisfactorily proved, although it is easy to demonstrate perivascular spaces in the liver of Man and of the Dog, and also, to some extent at least, to inject them. The cells in both these cases, as has been already mentioned, easily separate from the capillaries; in preparations preserved in alcohol especially, in which the capillaries as well as the cells shrivel, relatively wide empty spaces appear between the two, which are obviously artificial products. These spaces may be obtained of any width, according to the mode of preparation, in the liver of Man; the degree of shrivelling undergone by the cells may also vary, according to the nature of the antecedent disease, and the consequent constitution of the cells; as, for example, the amount of water they contain, and so forth. When, as in the liver of Man and of the Dog, the connection between the hepatic cells and the blood capillaries is only loose, a layer of fluid may perhaps in some instances collect between the two, especially in cases of vascular disturbance, by which the complete detachment of the cells from the capillaries, as the hardening proceeds, is still more favoured. All this, however, does not justify us in admitting the existence of perivascular lymphatic vessels; for on the same ground it might be maintained that, since a certain quantity of fluid exists between the fasciculi of the fibrillar connective tissue, each separate fasciculus is enclosed in a lymphatic vessel. The results of injection are also inconclusive; for the supposed perivascular lymphatic vessels have only been injected by extravasation. But whither must the injection pass, if it be driven with excessive force? What is more natural than that it should detach the easily separable hepatic cells from the blood capillaries, and insinuate itself between them? In the Rabbit their detachment does not occur, and hence no perivascular lymphatics can be injected in the liver of this animal; but we find that here the injection constantly bursts into and fills the blood capillaries.

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* *Centralblatt für die medicinische Wissenschaften*, 20th February, 1869.

The statement which has been made, that perivascular lymphatics can be injected in the liver of the Rabbit, is incorrect, and I have even found that no perivascular spaces can be demonstrated in that animal; a very important fact in opposition to their occurrence in the livers of others.

THE CONNECTIVE TISSUE OF THE LIVER.—The liver possesses superficial and deep fibrillar connective tissue. The former constitutes the capsule of the liver, the latter the sheath of Glisson. The *capsule of the liver* is a membrane, varying in thickness at different points, but usually of such tenuity that the substance of the liver is clearly visible through it. In those parts which obtain a peritoneal investment, a superficial "serous," and a deep fibrous, layer can generally be distinguished (Theile). The *deep connective tissue* forms an investment to the larger vessels, and incomplete septa between the lobules. No proper fasciculi of connective tissue penetrate into the interior of the lobules of a healthy liver, but there is an intralobular connective tissue, composed of a few scattered fibres which are partly applied to the capillaries, especially in the periphery of the lobules, and partly appear in the form of simple or branched fibrils, which are stretched between the capillaries, and assume more or less of the form of reticular connective tissue. Nucleated bodies which sometimes lie on the outer surface of the capillaries, are commonly considered to be connective-tissue corpuscles. The demonstration of the intralobular connective tissue is best accomplished in extremely fine sections of livers that have been moderately hardened in chromic acid; for here the hepatic cells fall out from the thinnest spots and from the borders, so that the capillaries and the fibres in question are completely isolated. Sections that are somewhat thicker should be shaken for a considerable time in the hardening fluid, or if still less successfully made they should be pencilled out.

His* considered the extremely fine striæ or plexiform systems of lines frequently visible on the wall of well-isolated capillaries, to be an adventitia capillaris, but was unable to discover any connective-tissue corpuscles in it. He also first directed attention to the delicate

* *Zeitschrift für wissenschaftliche Zoologie*, 1860, Band x., p. 340.

trabeculæ that, in capillary meshes from which the hepatic cells have been removed, sometimes appear stretching from one capillary to another, and are expanded at their points of attachment. Henle and Kölliker substantiate these facts, though Kölliker is inclined to regard them as capillaries in process of development or of retrograde metamorphosis. According to this observer also, in addition to connective-tissue corpuscles, there is an extremely small quantity of amorphous connective tissue. E. Wagner* first pointed out the presence of connective-tissue corpuscles within the lobules, and his statements have been corroborated by Engel-Reimers,† Kölliker, and Förster.‡ Henle, on the other hand, disputes the presence of the connective-tissue corpuscles, but considers that all the capillaries are accompanied by fibres of connective tissue, which are sufficiently thick when seen in section to present the appearance of dark granules. These differences in opinion are due to some extent to the circumstance that observers have not always stated whether the central or the peripheric portion of the lobule has been subjected to examination, whether the liver from which it was taken was healthy or diseased, and whether the subject was young or old. The frequently fusiform cells of the liver may also, in some instances, have been mistaken for the corpuscles of connective tissue.

The liver of Man exhibits such great variations in regard to its deep connective tissue, that, unless an extensive series of examinations are undertaken, it is very difficult to say what are really the natural relations. In adult Dogs the normal relations are as follows: The fibrillar interlobular connective tissue sends only a few thin and but feebly striated fasciculi into the outermost layers of the lobules. These cords immediately break up into fine completely homogeneous trabeculæ, which, on the removal of the hepatic cells, appear to extend tightly stretched from one capillary to another. Such homogeneous trabeculæ are frequently also found in other parts of the lobule, extended across the capillary meshes. Sometimes such a trabecula simply passes from one capillary to another; sometimes it divides in its course, and is attached by a forked extremity to one of the capillaries; and sometimes several trabeculæ spring

* *Oestreichische Zeitschrift für praktische Heilkunde*, 29 März, 1861.

† *Expl. micr. de tel. hepat. conjunct. Berol.*, 1860.

‡ Kölliker, *Handbuch der Gewebelehre*, 5th Edition, p. 438.

from the periphery of a capillary plexus, which coalesce towards the centre, and subdivide and anastomose in their course, so that in some instances a delicate plexus of extremely fine trabeculæ is formed, that presents in every respect the characters of reticular connective tissue. This form of connective tissue contains no nuclei; and inasmuch as the hepatic cells exhibit no trace of a membrana propria, this sparingly present reticular connective tissue constitutes, apart from the hepatic cells and the blood capillaries, the only formed or morphological element whose presence has been clearly demonstrated in the liver.

THE NERVES OF THE LIVER.—The tolerably numerous nerves entering the great fissure of the liver, and ramifying with the vessels contained in Glisson's sheath, are composed principally of non-medullated with a few medullated fibres, the latter always becoming less numerous as the fasciculi become smaller. The smallest fasciculi contain only non-medullated fibres. All demonstrable nerves lie on the outer side of the lobules. I have not succeeded in discovering any in their interior; and since we may easily satisfy ourselves, from an examination of very fine sections of hardened livers, that no fibres or other structures besides the hepatic cells, the capillaries, and the above-described sparing connective tissue are visible, we may conclude that if nerve fibres penetrate into the interior of the lobules they must be of extreme tenuity.

In a brief provisional communication, Pflüger has arrived at quite different results from the examination of the liver treated with perosmic acid. I also have made frequent use of this reagent, but hitherto have been unsuccessful in seeing the appearances he describes. The more extended account of his observations, about to be published, will, it is to be hoped, explain the cause of this discrepancy.

CHAPTER XIX.

LARYNX AND TRACHEA.

By E. VERSON.

A. Larynx.

Framework.—The changes in the form and disposition of parts that the modulation of the voice necessitates in the trachea, as the organ for the production of musical sounds, are effected exclusively by voluntary muscles, which, however, require firm points of attachment to enable them to act effectively. Such points are afforded by the cartilaginous framework, the composition and arrangement of the separate parts of which render a multiplicity of movements practicable, which vary in the different classes of animals with the requirements of their vocal capability.

The rudimentary trachea of the Proteus presents only a band of cartilage on each side; but from this, as Henle has demonstrated, there is developed, if we follow its variations through the ascending series of animals, by subdivision and outgrowth, and again by partial resorption, that complexity of structure which culminates in the form and powers of execution possessed by this organ in Man.

The division of the simple cartilaginous plate at the side of the trachea, found in the lower classes of animals, into the seven or more pieces present in the higher Mammals, necessitates also the development of a ligamentous apparatus to give support to the several parts; and hence the description of the framework of the trachea demands the consideration, not only

of the cartilage itself, but of the means by which the segments are connected together.

The cartilage of the trachea in Man partly belongs to the type of hyaline, partly to that of fibro-cartilage, and in the earlier stages of development possesses a tolerably active metamorphosis of tissue, the demands for which are supplied by appropriate bloodvessels, and regulated by nerves. At some few points the perichondrium gives off processes that penetrate into the substance of the cartilage, and consist of delicate connective tissue, with numerous fusiform cells, between which many vessels of different size may be distinguished, as well as a few nerve fibres. In the adult this direct connection between the cartilage and the vessels of the perichondrium either disappears altogether or becomes materially diminished.

With the advance of age the hyaline cartilage undergoes ossification, the change commencing usually at the age of forty years, though exceptionally much earlier, as at twenty. The process begins with the simple deposit of calcareous salts in the matrix, and spreads with tolerable uniformity from certain points of ossification. The limits of the ossification are consequently not very sharply defined. There then occurs a scattered punctiform precipitate in the matrix of the cartilage, which becomes constantly more and more dense, and ultimately blends with the uniformly calcified matrix. Near the margin of the ossified portion the cartilage cells appear still unaltered; but at a little distance from the margin, in the part which has been for some time ossified, they are characterized by numerous processes, giving them a stellate form, and they then present no points of difference from ordinary bone corpuscles. The fibro-cartilages, as a general rule, undergo no ossification with advancing age; an exception occurs, however, in the case of the arytenoid cartilages of the Dog, which become ossified.

To the series of pure fibro-cartilages belong the epiglottis, the cartilages of Santorini, of Wrisberg, and the inconstant sesamoid cartilages; to the pure hyaline belong the thyroid and cricoid cartilages, and the corpusculum triticeum; whilst, lastly, the arytenoid cartilages appear to be partly hyaline and partly fibrous.

The *cartilage of the epiglottis* presents numerous excava-

tions and fossæ on its posterior or inferior surface, which often even penetrate through its whole thickness, and then usually permit the passage of vessels and small nerves. The shallower depressions are occupied by fat cells or acinous glands, of which the latter are collectively situated on the posterior surface of the organ. The perichondrium, of course, follows all the hollows and inequalities of the cartilage. The epiglottis ossifies only in reptiles and birds, in which it is in intimate relation with the thyroid cartilage.

The *thyroid cartilage* exhibits a hyaline structure in general, though there are a few points where fibres appear between the cartilage cells. This especially occurs at the borders from which elastic bands of attachment extend to the hyoid bone and to the cricoid cartilage, and to a still greater extent in the re-entering angle at the level of the true vocal cords, the most external fibres of which run deeply into the cartilage, and to a certain extent divide it into three segments —a median, situated between the two vocal cords (*lamina mediana*, Halbertsma), and two lateral. In the newly born child another condition is exhibited, a similar segmentation into those parts being indicated, but only by the circumstance that, as in the adult, the more closely arranged cartilage cells of the median portion appear bounded on each side by a line, the concavity of which is directed outwards, of more scattered and uniform-sized cells. A complete tri-partition of the thyroid cartilage occurs only in birds. Lastly, fibrous bands may be found in the central portions of the thyroid cartilage of young animals, partly alone, and partly constituting a support for bloodvessels.

In regard to the *cartilages of Wrisberg*, it is well known that they sometimes break up into three or more rounded masses, which are sometimes arranged vertically one over the other, and sometimes on the same horizontal plane. The perichondrium investing the several nodules is elongated into bands that decussate with each other, so as to leave spaces occupied by acinous glands.

The *cartilage of Santorini* (*c. corniculata*) appears to be separated from the arytenoid cartilage only by a process of the perichondrium, which is distinguished from that investing

other parts by its softer nature, and by its containing a few scattered cartilage cells. It usually appears to consist of fibro-cartilage, but sometimes conceals a hyaline nucleus within the fibrous cortex.

Lastly, the central substance of the *arytenoid cartilages* exhibits a purely hyaline structure. Near their surface, however, they frequently become fibrous, and this occurs without exception at the point of attachment of the processus vocales and at the apex of the pyramid. In the Dog a remarkable development of cartilage may take place, extending to some distance from the arytenoid cartilages into the two vocal cords. In such cases a fibro-cartilaginous lamella of moderate width runs forward in the cords, which is continuous with a mass formed by the fusion of the cartilages of Santorini and Wrisberg with the arytenoid cartilages.

The mode in which the cartilages are united together so that movement is combined with great resistance to displacement is accomplished by means of *ligaments* or proper *articulations*. The former are everywhere continuous with the surrounding tissues, and are essentially composed of elastic with a few connective-tissue fibres, and in infancy are especially rich in fusiform cells. Near their attachment to the cartilages they usually contain cartilage corpuscles, which become more numerous towards the cartilage, and ultimately a transition into cartilaginous tissue occurs.

An articular mode of union exists between the cricoid and arytenoid cartilages, and between the cricoid and the thyroid cartilages.

The *crico-arytænoid articulating surfaces* are composed of hyaline cartilage, the somewhat small cartilage cells being closely arranged, and lying with their long axes parallel to the surfaces of the joint. The articular surfaces of the cricoid become to some extent fibrous at their periphery, *i.e.* at the line of attachment of the capsular ligament, the fibres extending into the joint from all sides, but becoming lost before reaching the centre. The capsule, on the other hand, contains cartilage corpuscles near its point of attachment, which extend into it from the cartilage. From behind and externally an interarticular substance penetrates into the joint which presents

a broad basis where it is connected with the capsule, whilst it becomes attenuated as it advances internally. It is usually composed of firm tense fibrous tissue containing a small number of large cartilage cells, but is not, like the rest of the internal surface of the capsule of the joint, invested by epithelium.

The capsule of the *crico-thyroid articulation* is principally composed of connective tissue which is prolonged over nearly the whole extent of the articular surface of the cricoid cartilage. Cartilage cells are disseminated throughout the tissue of the capsule. The accessory ligaments of this joint are relatively poor in elastic tissue.

Soft Parts.

The epiglottis is invested by a *mucous membrane* which, especially near the apex, is characterized by its delicacy and by its being comparatively loosely connected with the perichondrium; it contains numerous longitudinal elastic fibres, between which are spheroidal corpuscles with one or many nuclei, that are especially abundant at the sides of the bloodvessels and immediately subjacent to the epithelium. The free surface of the mucous membrane on the posterior surface of the epiglottis appears in transverse sections limited towards the epithelium by a sharply defined straight line, whilst anteriorly the contour line of the membrane is sinuous, and presents papillæ that project into the epithelium, of 0·7—0·18 of a millimeter in length, the larger examples of which terminate in two or even three points, and contain beautiful vascular loops. Inferiorly towards the entrance into the trachea the mucous membrane becomes thicker, is more sharply differentiated from the loose submucous tissue, and from this point downwards preserves a thickness of 0·1—0·15 of a millimeter, becoming somewhat thickened, however, in some instances, at the upper or false vocal cord.

The *epithelium* of the anterior surface of the epiglottis consists of well-marked laminated pavement cells, and is from 0·2 to 0·3 of a millimeter thick. It is much thinner posteriorly, only amounting to 0·06—0·1 of a millimeter. The deepest layer consists of delicate columnar cells arranged like palisades; above these is a layer of more rounded or polygonal

and somewhat flattened cells, forming a stratum Malpighii, before they become flattened into the superficial corneal lamina. Towards the cushion of the epiglottis the cylindrical basal cells become elongated, whilst the superjacent cell layers become correspondingly attenuated, and ultimately, with the persistence of the now elongated basal cells, entirely disappear; these last then acquiring cilia having a length of 0·005 of a millimeter, and becoming converted into ciliated cells. Between their attached extremities are numerous round or oval cells, and the new epithelial investment may attain a thickness of 0·15 of a millimeter, or more.

The transition of the epithelial formation of the anterior to that of the posterior surface of the epiglottis occurs in such a manner that the tesselated epithelium of the anterior surface

Fig. 124.

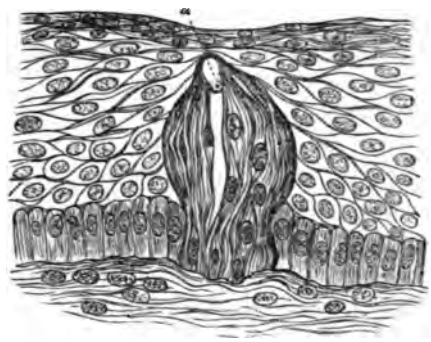

Fig. 124. Epithelium of the posterior surface of the epiglottis, with a bulb-like structure. *a*. Transverse section of the central canal.

invests the border of the cartilage, and then becomes suddenly attenuated. In the newly born child the entire posterior surface of the epiglottis is covered by a layer of ciliated epithelium amounting to 0·08—0·01 of a millimeter in thickness.

At about the second fourth of the posterior surface of the epiglottis, where the epithelium ordinarily presents its transition into the ciliated form, clavate, or in some instances pyramidal, structures are found, the apices of which approximate the horny layer, and give off a fine canal that reaches the surface either by pursuing a straight course or after making a

few coils. These structures consist of elongated epithelial cells of various width, with their, for the most part broader, bases attached to the mucous membrane, whilst their pointed extremities are directed to the free surface, forming a series of layers around a central tubular cavity. The cavity itself becomes remarkably attenuated at the apex of the bulb, immediately beneath the horny lamina, and is continuous with the above-named fine canal. Whether these structures are to be regarded as the excretory ducts of acinous glands I am unable from transverse sections to decide.

The epithelial cells of the epiglottidean mucous membrane undergo, when acted upon by certain reagents, a conversion into cup or goblet-cells, similar to those of the mucous membranes of other parts.

The submucous tissue of the anterior surface of the epiglottis is thicker and looser in texture than the posterior, and its fibres usually pursue two chief directions.

In the first place there are fasciculi that for the most part run circularly around the cartilage, and between these are longitudinal fibres running towards the base, which gradually preponderate over the former.

At the point of transition of the epiglottis into the tongue some of these longitudinal fibres radiate into the substance of the latter. The middle fasciculi of these fibres are composed of pure elastic tissue, and raise the mucous membrane into the glosso-epiglottidean folds which at the sides are again mingled with more loosely arranged connective tissue, the fasciculi of which frequently diverge to enclose fat cells. The direction pursued by this band of longitudinal fibres can be easily followed in the deeper layers adjoining the perichondrium of the epiglottis, from which at the same level the hyo-epiglottidean ligament takes origin, whilst a little lower it is continuous with the thyro-epiglottidean ligament. A few muscular fibres occur in the deeper layers belonging to the thyro-arytæno-epiglottidean muscle, which extends from the thyroid cartilage towards the borders of the epiglottis, or lies in the arytæno-epiglottidean folds. The submucous tissue of the posterior surface of the epiglottis becomes more abundant and more open in texture at its lower part, so that the loosely attached mucous

membrane in the portion corresponding to the inferior pointed extremity of the cartilage projects like a cushion. The fat cells and acinous glands are here very numerous, forming together masses of about one millimeter in diameter, with the excretory ducts running in a tolerably straight direction to the surface of the membrane. At the free extremity of the epiglottis the acinous glands are either only sparingly present or are altogether absent, but towards the lower part they occur in small groups arranged on either side of the middle line, and imbedded in the fossæ of the cartilage. Towards the epiglottidean cushion below, the groups become more frequent, of larger size, and their excretory ducts run in a straight direction through the epithelium; whilst those of the upper part are only straight till they reach the epithelium, when they turn at right angles to their former course, and sooner or later again bend to enter the epithelial coat, in order—as I imagine, though I have been unable to demonstrate the direct continuity of the parts —to terminate in the already-described bulb-like organs.

The *acinous glands* of the larynx are everywhere composed of a structureless membrane, lined by an epithelium, the cells of which have the form of truncated cones, and are attached by their broader extremities. The excretory ducts are lined by a layer of columnar epithelium, which, sometimes on the epiglottidean cushion, and on the lower surface of the false vocal cords, becomes ciliated. These excretory ducts are especially characterized by their large size, having a diameter in some instances of as much as 0·3 of a millimeter. The structureless membrane of the ducts may not unfrequently be obtained in an isolated condition, when large stellate connective-tissue corpuscles make their appearance attached to its outer surface, and with their long processes coiling spirally around it.

The ducts of the acinous glands on the posterior surface of the epiglottis of the Dog are sometimes lined by a double layer of cuboid cells.

The fasciculi of the submucous tissue of the arytæno-epiglottidean folds pursue the same direction as the folds themselves, and consequently invest the fasciculi of the thyro-arytæno-epiglottidean muscle, which, curving round the cartilago

corniculata of the same side, divaricate in these folds, and, adhering to their external surface, partly terminate there, and partly extend to the lateral border of the epiglottis, becoming inserted into the perichondrium. The transversely striated muscular fibres, that have a breadth of about 0·03—0·05 of a millimeter, terminate by the sarcolemma becoming attenuated to a thread, which, either with or without nuclear dilatations, is lost in the surrounding connective tissue, or between the fibres of the perichondrium.

The fasciculi of connective tissue of the submucous layer in the vicinity of the cartilages of Wrisberg become irregular, decussate and interweave with the processes of the perichondrium investing these cartilages, and form numerous spaces for the reception of the acinous glands, that are here so remarkably numerous as to cause the mucous membrane itself to project.

In the Sheep, Pig, Cat, and some other animals, lymph follicles are contained in the mucous membrane forming the fold at the orifice of the larynx.

Lower down the mucous membrane forms the fold of the upper or false vocal cords, the rounded borders of which hang loosely down, and beyond these is continued as the lining of the ventriculus Morgagni. At the fold of the upper vocal cord a portion of the highly elastic layer (fibrous layer), the direction of the fibres of which is here exclusively longitudinal, extends into the highly corpusculated mucous membrane; so that this layer is also, to a certain extent, folded. Other elastic fibres, running horizontally, and arising from the angle of the thyroid cartilage, and passing backwards, are interwoven in large numbers with the membrane at this point, partly terminating in the median raphé, partly curving downwards to cover the posterior angle of the ventricle of Morgagni. It cannot, however, be said that there is a proper superior thyro-arytænoid ligament, for the fibres do not pursue one direction exclusively, nor are they united into a ligamentous band; and a section made at right angles to the superior vocal cord exhibits only irregular fasciculi of elastic, mingled with connective-tissue fibres, which sometimes separate from, and sometimes coalesce

with, each other. In consequence of this disposition of the fibres, large interspaces occur, which are occupied by numbers of fat cells and considerable masses of glands. Both above and below, a few isolated fasciculi run directly into the longitudinal fibrous layer of the larynx.

In the Dog the elastic tissue of the superior vocal cord not unfrequently becomes converted into cartilage, the process of the arytænoid cartilage that runs forwards appearing to be prolonged into it. In this animal also the horizontal direction of the fibres is much more strongly marked, whilst the fasciculus, which in Man curves downward over the posterior angle of the ventricle of Morgagni, becomes quite an independent structure, causing the mucous membrane with which it is covered to project to a considerable extent, and producing the impression that the superior vocal cord is inserted along the floor of the ventricle. Where the above-mentioned conversion into cartilage occurs, the glands, for the most part, lie behind the cartilage, and traverse it to discharge their secretion into the ventricle.

A few small fasciculi of the external thyro-arytænoid muscle, sometimes even in Man, enter into the composition of the superior vocal cord, and then appear as an independent muscle (Musc., Santorini).

The margins of the arytæno-epiglottidean folds, throughout their whole extent, are covered with an epithelium composed of tesselated cells, which is continued over the opposed surfaces of the arytænoid cartilages, as far down as to the level of the lower vocal cords. In animals the mucous membrane presents papillary processes, similar to those that in Man are only found on the folds of the mucous membrane produced by the cartilagines corniculatæ, and which sometimes measure 0·35 of a millimeter in height, and 0·1 in breadth. On the other hand, the superior vocal cords, and in Man the walls of the ventricle also, are lined by ciliated epithelium, similar to that which has already been described as occurring at the base of the epiglottis. The glands within the ventricle break up into groups of much smaller size, all of which discharge their secretion by just such separate straight excretory ducts as are found on the opposed surfaces of the arytænoid cartilages.

In the *true vocal cords,* and especially at their free border,

the thin elastic tissue, which in the ventricle of Morgagni, separates the mucous membrane from the cartilage, undergoes a remarkable thickening from the presence of a compact prismatic band (the inferior thyro-arytænoid ligament), the chief portion of the fibres of which, attached in front to the angle of the thyroid cartilage below the notch, run backwards to the arytænoid cartilage.

The fibres of this cord appear to be collected into a single band at their anterior extremity only; posteriorly they separate at an acute angle into several fasciculi, which are inserted at different points. One of these applies itself above to the posterior angle of the ventricle, and thus extends towards a part of the superior thyro-arytænoid ligament, with which it interweaves. A second, which is the strongest, partly penetrates into the fibro-cartilage of the processus vocalis, and partly becomes attached at a higher level to the inferior spine of the arytænoid cartilage, and consequently covers the processus vocalis. A third, lastly, which occupies the lowest position, splits near the processus vocalis into five or six smaller bundles of fibres, which extend to the median surfaces of the arytænoid cartilages, to the inner side of the capsule of the crico-arytænoid articulation, and even as far as to the upper border of the lamina cricoidea. These different fasciculi are separated from one another by longitudinal fibres of connective tissue, which arise in the neighbourhood of the cart. corniculatæ.

All these elastic fasciculi unite anteriorly, as has been already remarked, into a compact, and consequently smaller, cord, which penetrates for some distance into the thyroid cartilage itself. Very near its attachment to this cartilage the inferior thyro-arytænoid ligament forms a rounded projection, which, in fine sections, appears as a dense felt of elastic fibres. This thickening is easily recognizable, even in newly born children; its chief constituent, however, here consists less of elastic fibres than of rounded and fusiform cells, which, with advancing age, continually increase in length. I have never observed any conversion into cartilage occur at this point.

In the Dog the upward arching fasciculus of the inferior thyro-

arytænoid ligament is as strongly marked as the downward curving fasciculus of the superior, so that it renders the mucous membrane prominent. It should further be mentioned that the differentiation between the true vocal cords and the thyro-arytænoid muscle is much better defined in Man than in animals.

The projecting border of the true vocal cord in Man is invested by a layer of tesselated epithelium, having a thickness of about 0·1 of a millimeter, which is rather suddenly replaced towards the ventricle of the larynx and the trachea by ordinary ciliated epithelium; whilst posteriorly it is continuous with the tesselated epithelium covering the arytæno-epiglottidean folds. The pavement epithelium of the vocal cords is indented on its deep surface by large papillæ, which have a breadth at their base of 0·03 of a millimeter, and project as much as 0·05 or 0·06 of a millimeter into its substance.

At the lower part of the glottis, and towards the trachea, both the epithelium and the mucous membrane become attenuated. The submucous tissue, on the other hand, increases in thickness on the anterior part of the larynx, in consequence of fibres joining it from the crico-thyroid membrane, and it is proportionately increased as it retreats from the mucous membrane under the prismatic belly of the thyro-arytænoid muscle. At this part it contains numerous glands in its substance, which have a remarkably flattened arrangement, presenting a large surface in proportion to their depth. About the level of the cricoid cartilage the glands are especially accumulated at the posterior surface of the larynx, where the submucous tissue also undergoes a considerable increase in thickness.

The *vessels* of the larynx present no peculiarities; the larger branches run in close proximity to the cartilaginous framework of the organ, or are deeply situated in the soft parts. The smaller branches extend towards the mucous membrane, and break up within it into a fine plexus.

Nor do the *nerves* present any characteristic features beyond the circumstance that they are unusually numerous. Branches of various size may be followed into the mucous membrane, but the precise mode in which they terminate is at present unknown. The muscular branches of the superior and of the

recurrent laryngeal nerves, previously to their ramification in the substance of the muscles, appear to be mingled with numerous ganglion cells. According to Luschka, the real termination of the nerves is effected by means of pyriform or oval corpuscles, having a diameter of 0·0035 of a millimeter, to each of which a fine axis-cylinder runs, that usually terminates in a slight enlargement.

B. TRACHEA.

The framework of the trachea is composed of from fifteen to twenty incomplete cartilaginous rings, which, being open behind, resemble a horseshoe in form. Variations of this form occur especially at the upper and lower extremities of the trachea, where the rings frequently divide, and join with the ring above or below; the enumeration of the individual rings is thus rendered very difficult.

Small masses of cartilage may occasionally be found scattered between the free extremities of the rings, and, like them, consist of hyaline cartilage. Similar masses occur sometimes in animals.

In the Dog, Cat, Sheep, etc., the cartilaginous rings represent, as in Man, segments of circles. In the quiescent condition they are almost in contact, whilst on contraction of the muscular layer they overlap each other, causing the mucous membrane to project into the lumen of the trachea in the form of longitudinal folds, having a breadth of from 3 to 4 lines.

Running from the lower border of the cricoid cartilage to the first ring of the trachea, as well as between the several rings throughout the whole length of the tube, are highly elastic bands, mingled with connective tissue, which bind the whole framework together. Numerous bands of a similar nature radiate also from the lower border of each ring into the submucous tissue.

The inner surface of the trachea is lined by a mucous membrane, having a thickness of 0·13 to 0·15 of a millimeter, characterized by the remarkable abundance of longitudinal plexuses of elastic tissue. This membrane is sometimes bounded internally by a thin hyaline layer, which has been regarded as

a basement membrane, on which again is an epithelial layer of ciliated cells, having a thickness of 0·06—0·075 of a millimeter.

The submucous tissue, like the tissue of the mucous membrane, is marked by the predominatingly longitudinal direction pursued by its fibres, which are for the most part composed of connective tissue, becoming progressively mingled with more elastic fibres towards the outer surface. In the posterior portion of the trachea, and extending between the anterior surfaces of the free extremities of the cartilage, there is a thick (0·8—1·2 of a millimeter) transverse layer of organic muscular fibres, inserted by means of small delicate tendons into the perichondrium of the cartilaginous rings, or more rarely lost in the mucous membrane.

This muscular layer is intersected or segmented by strong bands of connective tissue, several of which usually correspond to each cartilaginous ring. These septa are accompanied by vessels and nerves which supply the mucous membrane from behind. Not unfrequently short longitudinal muscular fasciculi lie on the outer side of the transverse muscular coat, which arise from, and terminate in, the above-named septa, and serve as clamps for the transverse fasciculi. Lastly, on the outermost surface there is a layer of longitudinal connective tissue (fibrous layer).

Similar but much stronger muscular fasciculi occur in the trachea of the Dog and Cat, and when these contract they cause the rings to become imbricated, or to overlap each other, so that when divided horizontally the sections of two adjacent rings are obtained, separated by elastic tissue, and arranged concentrically.

In these animals, as well as in the Rabbit, Sheep, etc., the transverse muscular layer presents the peculiarity of extending far beyond the extremities of the cartilage, and of being inserted into their *external surfaces*. It invests quite as much as one-third of the circumference of each ring, and can contract so powerfully as to bring their free extremities into contact, or even to make them overlap.

The trachea is abundantly supplied with acinous glands, which form anteriorly and laterally a continuous layer, that does not appear to be interrupted even over the most convex

part of the rings. At the posterior surface of the trachea they form several layers,—one being situated between the mucous and muscular coats, another in the muscular coat itself, and others behind this coat, so that their excretory ducts, which run straight to the surface, perforate the muscular coat.

The *vessels* form superficial plexuses in the tracheal mucous membrane, similar to those of the larynx.

The mode in which the nerves terminate is still unknown. In the posterior fibrous membrane they present ganglionic swellings of considerable size, and of rounded oblong form, the longest diameter of which is parallel to the axis of the nerve. Their breadth amounts to 0·2 of a millimeter, their longitudinal diameter is about from two to three times greater.

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CHAPTER XX.

THE LUNGS.

By FRANZ EILHARD SCHULZE.

I. The Lungs of Mammals.

From the bronchus, or free branch of the trachea, that enters each lung a system of tubes with solid and smooth walls is developed. These tubes ramify in an arborescent manner throughout the substance of the organ, and are termed *the bronchia*. From the primary trunk there originate in the first place, by a process of dichotomous division at acute angles, a number of diverging and successively smaller branches, which, after having attained a certain calibre, amounting in Man to about four millimeters (1-6th inch), almost completely cease to divide in this manner, but, constantly diminishing in size, continue in nearly a straight line to the surface of the lung, and give off spirally from their sides a series of small branches at an angle of 45°, which likewise pursue a straight course. The lateral branches springing in a similar manner from these last again branch with dichotomous, but almost perfect rectangular, ultimate subdivision. In consequence of this, as well as of the circumstance that one of the two branches at each division maintains the direction of the original trunk, whilst the divisions for the most part take place in planes alternately at right angles to each other, a peculiar zigzag course is presented by the smallest bronchi, which ultimately having a diameter of 0·3 to 0·2 of a millimeter, and even in the smallest Mammals, as in the Mouse, Bat, etc., not less than 0·1 of a millimeter, open into the *respiratory cavities*. These are

cylindrical passages which terminate cæcally after dividing dichotomously at acute angles, from two to four times, at a distance of 2—4 millimeters from each bronchial extremity. They present small gradually expanding or funnel-shaped terminal processes, and similarly pedunculated short lateral branches, both of which, on account of their constricted entrance and wide bases, are termed infundibula. [Open plexiform communications between adjoining air passages were first erroneously stated to exist by Bourgery,* and subsequently by Adrian,† Williams,‡ and others.] These passages, however, do not, like the bronchia, possess uniformly thick, solid walls, but are beset with numerous small polyhedric cavities, with rounded angles and borders, that are in immediate contact with each other, and opening into the lumen of the passage are called the alveoli. These are so closely arranged, both on the lateral and terminal processes of the infundibula, that only an extremely small portion of the parietes of the passages is formed by the free borders of the septa of the alveoli, but in by far the greatest part by the walls of the alveoli themselves. I would therefore name them *alveolar canals or passages.*

[Intralobular bronchial ramifications (Addison); lobular passages (Todd); intercellular passages (Rainey). Whilst according to the more popular German text-books the infundibula constitute the terminations of the divisions of the bronchia, I find descriptions of the structure of the parenchyma of the lung, similar to those which I have here given as the result of my own observations, have already been published by Lerebouillet,§ Addison,|| Rossignol,¶ and Le Fort;** also (putting aside the open retiform communications of the passages there maintained) in the article by Dr. Williams, on the Organs of Respiration, contained in Todd's Cyclopædia of Anatomy and Physiology, Vol. v., 1859; and by a few other English writers.]

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* *Gazette des Hopitaux*, Juillet, 1842.

† *De subtil. structura pulmonum*, 1847.

‡ Todd's *Cyclopædia of Anatomy and Physiology*, Vol. v.

§ *Anatomie Comparée de l'Appareil Respiratoire*, 1838.

|| *Philosophical Transactions*, 1842.

¶ *Recherches sur la Structure intime du Poumon*, 1846.

** *Recherches sur l'Anatomie du Poumon chez l'Homme*, 1859.

The calibre of these passages, so far as it is determined by the free borders of the alveolar septa, amounts in adults to 0·4—0·2 of a millimeter; in medium-sized Mammals, as the Pig,

Fig. 125.

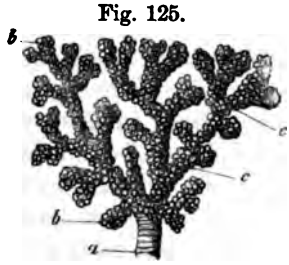

Fig. 125. System of alveolar passages, with infundibula, from the margin of the lung of a Monkey (Cercopithecus), injected with quicksilver. Magnified 10 diameters. *a*, Terminal bronchial twig; *b b*, infundibula; *c c*, alveolar passages.

Dog, and Cat, 0·2—0·15 of a millimeter; in the Rat, about 0·1; in the Mouse and Bat (Plecotus auritus), from 0·1 to 0·06 of a millimeter. The chief trunks are always somewhat larger than the subdivisions. The diameter also, in Man at least, increases with age.

Fig. 126.

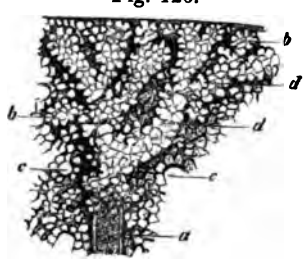

Fig. 126. Section of the lung of a Cat, injected with alcohol, and hardened. Magnified 12 diameters. *a*, Terminal bronchial twig; *b b*, infundibula; *c c*, transverse section of alveolar passages; *d d*, longitudinal section of alveolar passages.

The alveoli themselves, which on a transverse section of an air passage or infundibulum are seen to be radially arranged, and to vary from four to eight in number, are usually hemispherical

in newly born Mammals, but subsequently, from mutual pressure, become polyhedral. They are most shallow, whilst they are at the same time separated by tolerably thick septa, in the first portions of each system of alveolar passages that have been already described as constituting the immediate continuation of the smallest bronchial branches; on the other hand, they are deepest, and only separated by thin septa, in the terminal processes or infundibula, and pre-eminently so at their fundus. The length and breadth of alveoli of moderate depth are about equal. In those parts of the system of alveolar passages in which the diameter of the alveoli is least subject to variation the breadth constantly increases with age, whilst in advanced age the depth diminishes. The diameter of the alveoli in Man during the middle period of life amounts upon the average to 0·15 of a millimeter. Soon after birth it varies from 0·10 to 0·08 of a millimeter, in moderately advanced age (Woman, sixty years of age), the breadth is 0·25—0·4, and the depth 0·1—0·2 of a millimeter. The alveoli of the larger domestic animals present very similar dimensions, but they are much less in the smaller species. Thus I found the breadth of the alveoli in Rabbits to measure on the average 0·05; in the Rat, 0·04; and in the Mouse and Bat, 0·03—0·02 of a millimeter. The four to six-sided orifices of the alveoli, with their rounded angles, are generally rather smaller than the alveoli themselves, partly on account of the radial arrangement of the air cells, and partly on account of a slight thickening of the free borders of the alveolar septa.

In the description of the structural characters of the several parts it will be advantageous to separate that of the bronchia which are destined only for the conduction of air, from that of the parenchyma of the lung, consisting essentially of the alveoli, which is subservient to the interchange of gases between the air and the blood.

The *bronchia* of Mammals present remarkably similar histological features, the tubes of equal diameter having in general an analogous or identical structure. On the other hand, considerable differences exist coincidently with variations in size.

In the larger bronchia, down to those that do not exceed one millimeter in diameter, which may be first described, four

structurally distinct layers are distinguishable, independently of the tunica adventitia, which is composed of a variable amount of loose fibrillated connective tissue that contains here and there small masses of fat, and serves to connect the bronchia with the adjoining tissues, as with vessels, lymphatic glands, nerves, and alveolar tissue. The outermost of these layers, which constitutes more than half of the entire thickness of the wall, is the *external fibrous layer*, chiefly composed of dense fibrillated connective tissue, with imbedded cartilaginous plates. These last, so important in conferring firmness and elasticity on the bronchial tubes, still preserve in the primary branches, as in the bronchia themselves, the form of flattened semi-circles; they do not however, any more than in these, present a posterior defective portion, closed only by membrane; but, distributed over every part of the tubes, form a peculiar framework for supporting and strengthening them.

Fig. 127.

Fig. 127. A portion of the transverse section of a human bronchial tube, having a diameter of six millimeters, magnified thirty diameters. *a*, External fibrous layer; *b*, muscular layer; *c*, internal fibrous layer, with the hyaline basement membrane; *d*, epithelial layer.

To these semi-circular cartilages, the sharp borders of which in many animals are in immediate contact with each other, or, as in the Pig, even to some extent overlap, irregularly angular plates provided with short processes quickly succeed in Man; though in large animals, as the Cow and Horse, these do not appear until the bronchi have undergone several divisions.

The plates are then irregularly distributed, become gradually smaller, and separated by wider intervals, until they are completely isolated, and are chiefly found at the angles of division in the form of thin discs or clasps, finally disappearing in bronchia of less diameter than 1·5—1 millimeter. In very small Mammals, as in the Mouse and a few Bats,—*e.g.*, Vesperugo pipistrellus, in which the largest bronchia scarcely attain this size,—the cartilage may be altogether absent in the lungs.

A peculiar structure is presented by the bronchial cartilages in consequence of the following special arrangement of the numerous cells contained in the hyaline matrix. Whilst the flat cake-like cells of the cortical layer of the cartilage-plate are everywhere placed with their broad surfaces parallel to that of the lamina, the more rounded internal cells, which often form elongated groups, being held together by the so-called secondary cartilage capsules, are arranged in rows perpendicular to the surface; so that if we particularly examine the solid matrix of the cartilage, the two cortical layers arranged parallel to the terminal surfaces appear to be connected by transverse braces.

The fibrous tissue constituting a perichondrium to the cartilage where this is present, consists of closely arranged longitudinal fasciculi of connective tissue traversed by thinner circular layers, the two being even occasionally disposed in alternate laminæ, especially in the outer part of the membrane. It contains also longitudinal plexuses of fine elastic fibres, which become thicker and more abundant, where they extend from the thin border of one cartilage to the next, connecting the two in the direction of the long axis of the bronchia.

Whilst small masses of fat are found to be more or less abundantly distributed in the outer portion of this fibrous layer, the inner presents *mucous glands*, the number and size of which diminish in a proportion corresponding with that of the tube. These occupy in the larger bronchia, not only the intervals of the cartilages, where the parietes of the tube are composed of fibrous membrane by which their growth is unimpeded, and where they often attain a considerable size, extending far into the outer layer of the membrane, but also on the inner surface

of the cartilaginous plates, where their growth is restricted, and they consequently assume a flat cake-like form. In the smaller bronchia they only occur between the cartilages, and with the further division of these tubes become continually smaller, until, with the disappearance of the cartilages, they also entirely cease. From each of these glands a straight duct lined with columnar epithelium, which especially in old people may present at some part of its course a flask-like dilatation, leads to the free internal surface of the bronchial tube, where it opens by a trumpet-like orifice.

To the external fibrous layer succeeds the *muscular layer*, consisting of compact circularly arranged fasciculi of smooth muscular tissue. Although this layer, on account of its presenting rounded sections of isolated circular fasciculi, cannot be described as a tube with smooth and even parietes, yet the muscular bundles are applied so closely to one another, and communicate so frequently in a plexiform manner, that upon the whole a continuous layer is produced, the thickness of which is usually proportionate to the diameter of the bronchial tube. In those parts of the largest bronchi in the Horse which are free from cartilage, its thickness amounts to about 0·5 of a millimeter; in Man, 0·3; in the Dog, 0·2—0·1; and in the Rat, to 0·005 of a millimeter. In the bronchia of Man not exceeding four millimeters in diameter its thickness amounts to 0·1 of a millimeter; in those of two millimeters' diameter, to 0·05 of a millimeter. Beneath the cartilages the muscular layer is usually somewhat thinner.

In opposition to the two layers above described, which in transverse sections of the bronchia present the form of annular zones of tolerably equable thickness, the immediately succeeding *internal fibrous layer* offers on the same view a regular alternation of thick and very thin parts, giving a sinuous outline to the inner surface. This is due to the presence of from fourteen to twenty longitudinal elevations whose height is dependent on the degree of development of the whole layer, which again stands in a certain relation to the diameter of the bronchia. Thick longitudinal elastic fibres constitute the most characteristic and essential elements of this layer; they, however, do not form a stratum of uniform thickness,

but are united into fasciculi accumulated beneath the longitudinal folds. The stroma is composed of a loose form of connective tissue with delicate fibres, for the most part running longitudinally, and which towards the inner surface becomes con-

Fig. 128.

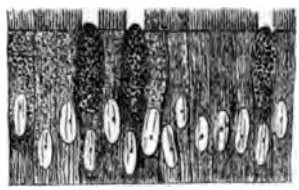

Fig. 128. Epithelium of a bronchial twig 4 millimeters in diameter, from the Dog, recent. Magnified 320 diameters.

densed into a hyaline layer. Upon this last or so-called basement membrane rests the *ciliated columnar epithelium* that invests all bronchia of the sizes that are now under consideration.

Intermediate to the ciliated cells, which in the larger bronchia of Man are about 0·08 of a millimeter in height, but are somewhat flattened in the smaller, and the medium-sized cilia of which strike towards the outlet of the tubes, *cup, goblet, or chalice cells*, of which I first gave a description, are distributed with tolerable regularity* and in considerable numbers. When these are carefully examined in perfectly fresh specimens, the whole theca may be seen to be filled with a mucous mass, through which numerous highly refractile granules are distributed, and which projects from the upper rounded opening of the cell in the form of a small ball, that sometimes becomes altogether detached. In addition to these, apparently membraneless and probably young cellular elements of rounded or indefinite form, are here and there found scattered between the usually attenuated or irregularly dilated attached extremities of the columnar cells which they are destined to replace.

The principal difference existing between the larger bronchi that have just been described and those whose diameter does

* M. Schultze's *Archiv für Mikroskop. Anatomie*, Band iii., p. 192, *et seq.*

not exceed one millimeter, is in the structure of the outer fibrous layer; for independently of the almost total absence of cartilage and of mucous glands, this becomes so remarkably attenuated in the smallest bronchia, that its thickness in Man does not exceed from 0·4 to 0·02 of a millimeter, and near their terminations almost entirely disappears. The external fibrous layer is here composed of longitudinal fasciculi of connective tissue, with a few elastic fibres interspersed amongst them, and running in the same direction. The succeeding muscular layer, with its circularly disposed smooth muscular fibres, becoming gradually thinner, breaks up ultimately in the finest bronchia into isolated circular bands, separated by intervals of greater or less width, which often consist of only a single layer of muscular-fibre cells interwoven with fine elastic fibres, that pursue a similarly circular direction.

The compact bundles of longitudinal elastic fibres, so charac-

Fig. 129.

Fig. 129. Part of a transverse section of a bronchial tube from the Pig, having a diameter of 0·4 of a millimeter. Magnified 240 diameters. *a*, External fibrous layer; *b*, muscular layer; *c*, internal fibrous layer; *d*, epithelial layer; *f*, one of the surrounding alveoli.

teristic of the inner fibrous coat of the larger bronchi, are continued into the smaller branches, where they run in the form of closely compressed fasciculi with a clear delicately fibrous basement membrane on the inner side of the tunica muscularis,

and in the longitudinal folds that are here present. The internal epithelial investment at first consists of ciliated epithelial cells with interspersed cup cells, similar to those with which we are already familiar in the larger bronchia. But as the termination of the smallest bronchia is approximated, the epithelial cells gradually become lower, so that after a little while their height does not materially exceed their breadth, and they may even ultimately assume a flattened form. Near the point of transition of the bronchia into the alveolar passages the cells lose their cilia, and the cup cells cease to appear.

The nutrition of the bronchia is effected by means of *capillary plexuses*, the meshes of which are irregularly arranged in the outer fibrous layer, circularly in the muscular, and longitudinally in the internal fibrous layer. The supply of blood is chiefly derived from the branches of the bronchial artery distributed in the adventitia and external fibrous layer; the ultimate bronchia only receiving here and there branches from the pulmonary artery, the capillaries of which anastomose with those of the bronchial arteries. The blood that has become venous in the capillary plexuses on the walls of the *larger* bronchia, alone enters the corresponding bronchial vein running towards the root of the lung; that of the smaller bronchia flows directly into the pulmonary veins.

Lymphatic vessels are abundant, especially upon the internal layer of the bronchia, the internal fibrous investment of which they traverse to pass towards the roots of the lung, where they enter the lymphatic glands that are there situated.

Small scattered ganglia that were first discovered by Remak, are found in the course of the *nerves* proceeding from the plexus pulmonalis, which ramify upon the bronchia, and are in great measure destined for the supply of the smooth muscular tissue that is here so abundantly present.

The structural characters of the *alveolar tissue* of the lungs of all Mammals are, like their bronchia, essentially similar.

The lateral walls of the contiguous alveoli of one and the same infundibulum or alveolar passage, uniformly coalesce to form thin

membranes, the alveolar septa. This, however, though common, is by no means constant in the case of the walls of adjacent alveoli belonging to different infundibular or alveolar passages. These are usually separated by uniform thin layers of loose fibrous interstitial connective tissue. Stronger septa of the same kind in the lungs of all Mammals divide off polyhedric portions of the alveolar parenchyma which are known as *lobuli*. As a general rule the size of these diminishes with that of the animal: in Man their diameter varies from 0·5 to 1 centimeter, and their irregularly polygonal boundaries, with four to six sides, are faintly seen as it were in transverse section through the pleura, as well as in sections made through the substance of the lung. The interstitial connective tissue of the parenchyma of the lung is firmly attached on the one hand to the pleura, and on the other is directly continuous with the investing and connecting loose adventitious fibrous tissue of the bronchia, vessels and nerves.

The fundamental layer of the alveolar wall is composed of a transparent structureless membrane, that only here and there, and especially in the thicker parts, exhibits a distinctly fibrous character; whilst sparingly distributed through it are elongated oval connective-tissue corpuscles without any noticeable surrounding granular area. This transparent layer is traversed by numerous elastic fibres, the peculiar arrangement of which principally confers upon the pulmonary tissue its characteristic appearance under the microscope. The elastic tissue occurs in greatest abundance in the main trunks of each infundibular system. In this situation annular bundles of strong elastic fibres are found, not always forming complete circles, which surround and in great measure compose the free thickened borders of the strong septa between the lateral groups of alveoli; these are especially well developed as the septa of bifurcation of the whole infundibulum, and also constitute the invariably somewhat constricted orifices of the lateral and terminal infundibula. From these compact bands of strong elastic fibres thinner fasciculi are given off, which serve on the one hand to support the borders and angles where several alveoli meet, and on the other form a border to the rounded polygonal orifices of the several alveoli, whether these open directly

into the passages, or first unite in the infundibula. Delicate isolated elastic fibres extend from these again, which divide dichotomously, and unite to form arches distributed in a retiform manner over the alveoli.

Fig. 130.

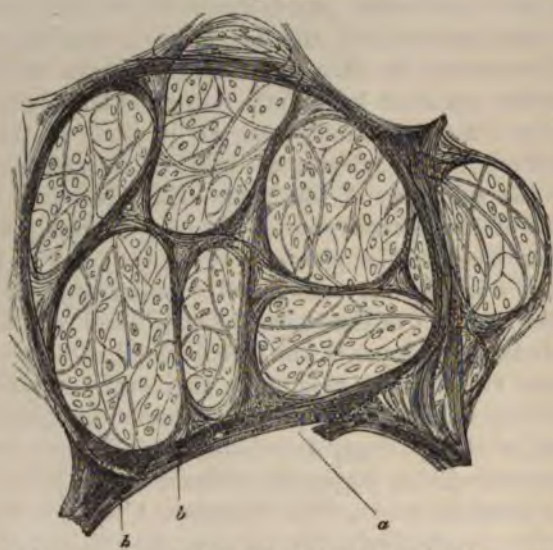

Fig. 130. Section made through a lateral infundibulum. From the lung of an adult Man, injected and hardened by maceration in alcohol containing a little acetic acid. *a*, Orifice of the infundibulum in the alveolar passage—the upper border has been partially removed by the cut; *b b*, nuclei of smooth muscular fibres. Magnified 80 diameters.

The septa for the most part projecting into the lumen of the alveolar passages, especially in the first portions of the main ones, where their free margins can still be regarded as a direct continuation of the bronchial wall, contain here and there between the more superficial layers of elastic fibres delicate scattered bands of *smooth muscular tissue* which often consist merely of isolated fibres imbedded in a delicate connective tissue. The membranous walls of the alveoli themselves are entirely *destitute of muscular tissue*, nor have I been able to

discover any muscular fibres in the more compact borders of the individual alveolar septa.*

The *respiratory capillaries*, the importance of which is so great for the due performance of the function of the lungs, are connected in a peculiar manner with the walls of the alveoli. They proceed from the branches of the pulmonary artery, which at first run with the bronchi imbedded in their tunica adventitia and external fibrous layer, and subsequently in the interstitial connective tissue of the lobuli and alveolar passages, and conduct the blood, after it has become arterialized, to the primary branches of the venæ pulmonales which are usually situated on the opposite side of each entire group of alveoli. These venous trunks, in their recurrent course, then usually accompany the pulmonary arteries, or more rarely run separately through the tissue of the lungs. Where the alveolar wall is surrounded by a compact layer of fibrous connective tissue, as at the extreme boundaries of the several lobuli, especially beneath the pleura, the rounded-angled, oval, or circular meshed plexus is so distributed in plane or flat arched expansions on the inner surface of the connective-tissue wall, that the capillaries only lie with a small portion, or at most one half, of their diameter imbedded in the basement membrane; the remainder of their wall projecting into the lumen of the alveolus.

But where, as in the greater number of instances, the walls of the adjacent alveoli have become fused into a thin membrane, the originally double layer of capillaries, each lying on the inner side of the membrane of their own alveolus, but now brought into immediate contact with one another, combine to form a single intricate plexus, owing to the development of innumerable anastomoses which traverse the common membrane, the meshes of which are very narrow, not exceeding 0·001 of a millimeter in Man, and but slightly narrower in smaller

* Whilst most anatomical writers have, like myself, been unable to discover smooth muscles in the alveolar walls, their presence has been asserted and described by Gerlach, *Gewebelehre*, p. 248; Moleschott, in his *Untersuchungen*, Band vi., p. 390; Colberg, *De penitiore pulmonum structura*, Halis, 1863; Hirschmann, Virchow's *Archiv*, Band xxxvi., 1866; and Piso-Borme, Moleschott's *Untersuchungen*, Band x., 1867.

animals; whilst they no longer lie on the same plane, but frequently running through the septal wall project sometimes into one and sometimes into the other of two contiguous alveoli.

If the course of the capillaries be followed in transverse sections of such alveolar septa, they will be seen to form loops, projecting now on this, and now on that side. These appear

Fig. 131.

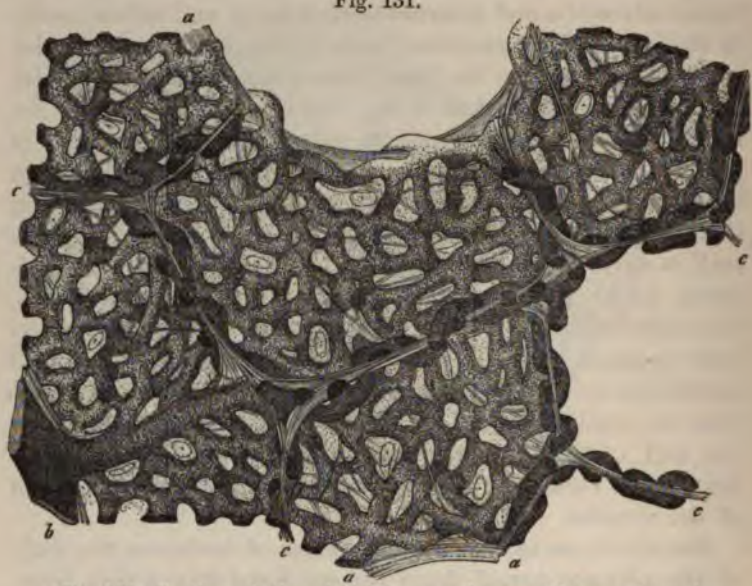

Fig. 131. Section of the alveolar parenchyma of human lung, injected from the pulmonary artery. *a a*, Free margins of the alveoli; *b*, small artery; *c c*, vertical walls of alveoli divided transversely.

most tortuous when the vessels are very fully injected and the alveoli are not much distended; whilst with full dilatation of the alveoli they lie more closely applied to the walls, though the greater part of their circumference even then projects freely into the interior of the alveolus. That these free surfaces of the capillaries are, in many parts at least, destitute of an independent investment of connective tissue, can be most easily demonstrated in the loops running round the free borders of the alveolar septa. The diameter of the capillaries does not materially vary with the size of the animal, but amounts in

the adult Man, when they are moderately distended, to 0·006—0·008 of a millimeter.

Each alveolus does not possess a separate and independent artery and vein, but the capillary plexus proceeding from a terminal arterial twig is usually distributed to several contiguous alveoli before it gives origin to a vein, at the point of transition of the terminal bronchia into its system of alveolar passages. In the smaller bronchia themselves, and immediately beneath the pleura, numerous anastomoses occur between the capillaries of the pulmonary artery and those of the bronchial arteries.

The *lymphatics of the alveoli*, according to the observations of Wywodzoff* on the lungs of Horses and Dogs, commence in small anastomosing lacunæ destitute of proper coats, situated in the fibrous alveolar wall; the larger trunks run in the direction of the elastic fibres, and subsequently follow the course of the capillaries, yet not so strictly but that they frequently cross the latter, and form large lacunæ in their meshes. From these rootlets the *deep-seated* lymphatics † arise on the one hand, which, accompanying the bronchi and vessels, extend to the root of the lung; and on the other the *superficial* lymphatics, which, lying close beneath the pleura, form a plexus investing the extremities of the lobuli, and in Man partly run towards the tubes, and partly dip in at certain points to communicate with the deep plexus.

The inner surfaces of the alveoli, as well as the whole of the infundibula and alveolar passages, lastly, are invested by a *continuous*, and in the fœtus homogeneous, *epithelium*. In adult Mammals, however, it is *not homogeneous*.

In the alveoli of mature fœtuses a uniform layer of contiguous flat four to six-angled epithelial cells is found, each of which possesses a membrane and granular contents, with a clear spherical nucleus; but in all individuals that have respired, even for a short time, a few epithelial cells may be discovered considerably enlarged and brighter, and with their granular

* *Wiener Medizinische Jahrbücher*, Band xii., p. 1.

† These also receive their lymph supply from the bronchia, and have already been noticed.

contents no longer visible, whilst the previously sharply-defined nucleus has become very pale.

In the alveoli of older animals,* the polygonal or irregularly spheroidal epithelial cells, with their granular contents and clear round nuclei, appear to be quite isolated, or arranged in small groups of two or four (seldom more) between *large transparent thin structureless plates, either irregularly angular in form, or with sinuous outlines*, which originate in the further

Fig. 132.

Fig. 132. The bottom of an alveolus, as shown in a section made parallel to the pleura from the lung of a Child injected with solution of nitrate of silver. The Child had been born at the eighth month, and had lived two days. Magnified 500 diameters.

development in quite young animals, and with the above-mentioned changes, of the epithelial cells of the original structure, and probably by the pressure of the rising capillaries, and the tension of the enlarging alveoli; perhaps also, as Elenz main-

* I have employed the Cat, Dog, Rabbit, and Calf as subjects of investigation. The thick pleura, and the impossibility of obtaining the lungs of Man sufficiently fresh, seriously interfere in his case with the treatment by means of silver.

tains, by the fusion of contiguous epithelial cells.* All the borders and edges of the framework of the lung projecting into the lumen of the air-passages, the free borders of the

Fig. 133 A.

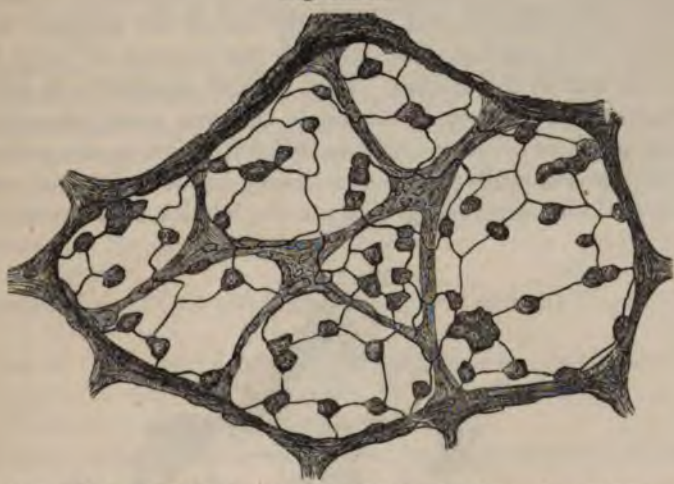

Fig. 133 A. Fundus of a peripheral infundibulum, situated immediately beneath the pleura. From the lung of an adult Cat, injected with solution of nitrate of silver.

alveolar septa, the more compact septa of contiguous groups of alveoli, the margins of the infundibular orifices, as well as the

* The results of my researches on the epithelium of the alveoli of the mammalian lung, which are here briefly given, agree in all essential points with those of Elenz (*Wurzburger naturwiss. Zeitschrift*, Band v.), Eberth (*idem*), C. Schmidt (*De l'epithelium pulmonaire*, Diss. 1866), and Colberg (*Deutsches Archiv für klinische Medicin*, Band ii.). The existence of an epithelial lining to the alveoli is positively denied by some writers, as by Addison, Remak, Rossignol, Reinhardt, Schröder van der Kolk, Adriani, Radclyffe Hall, Schultz, Gerlach, Williams, Waters, Deichler, Zenker, Bakody, and Henle. A few, as J. Arnold and Hertz, admit an interrupted epithelium, the nucleated cells of which are only present in the meshes of the capillaries, but do not cover the capillaries; whilst others, again, as E. Wagner, O. Weber, L. Meier, Chrzonszczewsky, Hirschmann, Baier, and Piso-Borme, describe an epithelium completely uniform in character, and composed of polygonal nucleated cells lying in immediate contact with each other.

edges at the points of dichomotous division of the whole series of air-passages, are invested by these thin transparent plates, the boundary lines of which, brought into view by the action of solution of nitrate of silver, for the most part cross them transversely. The granular epithelial cells are never situated *upon* the capillaries, but constantly invest the alveolar wall within their meshes; but so that the number of cells far exceeds that of the meshes. They exhibit, especially in adult Men, more rarely in other Mammals, the same small *spheroidal, black, pigment granules, that in all but children* are present in the alveolar walls; more abundantly in the interstitial connective tissue intervening between the lobules of the alveolar

Fig. 133 B.

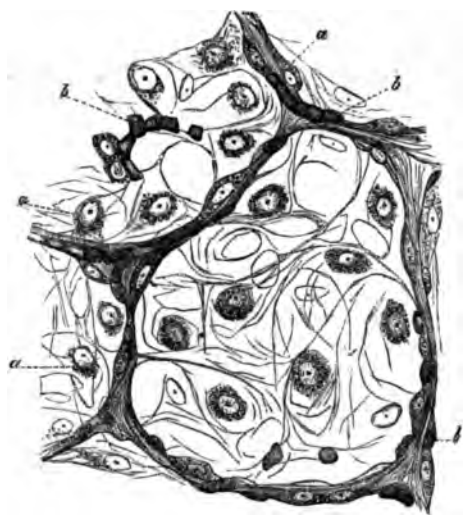

Fig. 133 B. Alveolus from the lung of a Cat, filled and hardened in Müller's solution. *a a*, Epithelial cells with granular contents; *b b*, capillaries with blood corpuscles. Magnified 300 diameters.

parenchyma accompanying the bronchia and vessels; especially abundant in the bronchial lymphatic glands; and usually grouped into rounded or stellate masses around clear nuclei. More rarely they are diffusely scattered, but always confer upon the lungs of adults their peculiar spotted black appearance.

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II. THE LUNG OF THE BIRD.

The *main pulmonary air passage* in Birds is continuous in a straight line with the free bronchus of each lung, traversing it from before backwards, and ultimately opening with a wide orifice into the abdominal air sac. It gives off lateral bronchial tubes, which, with their simple feather-like lateral branches, extend to the surface of the lung immediately beneath the accessory sheath of connective tissue, with which they partly fuse and partly become continuous with air sacs. From the internal surface of the membranous walls of these bronchia situated immediately beneath the surface of the lung, simple, slightly elevated, and smooth septa project, which unite in a retiform manner, so that the meshes circumscribe alveolar or honeycomb-like areas. From all the surface in contact with the parenchyma of the lung, as well as from some parts of the main air passage and at right angles to it, the *pulmonary tubes*, or *air canals* (canaliculi aeriferi) are given off. These are long tubes, the external surface of which presents an

hexagonal form on section in the bird, whilst their voluminous walls contain the true respiratory tissue, and constitute the principal portion of the entire lung. They run parallel and in close contiguity to each other; at first in a straight, but subsequently in a sinuous or zigzag direction, whilst they frequently communicate by anastomosing branches. Their internal free surface is circular on section, and is characterized by the presence of strong membranous annular ridges, which

Fig. 134.

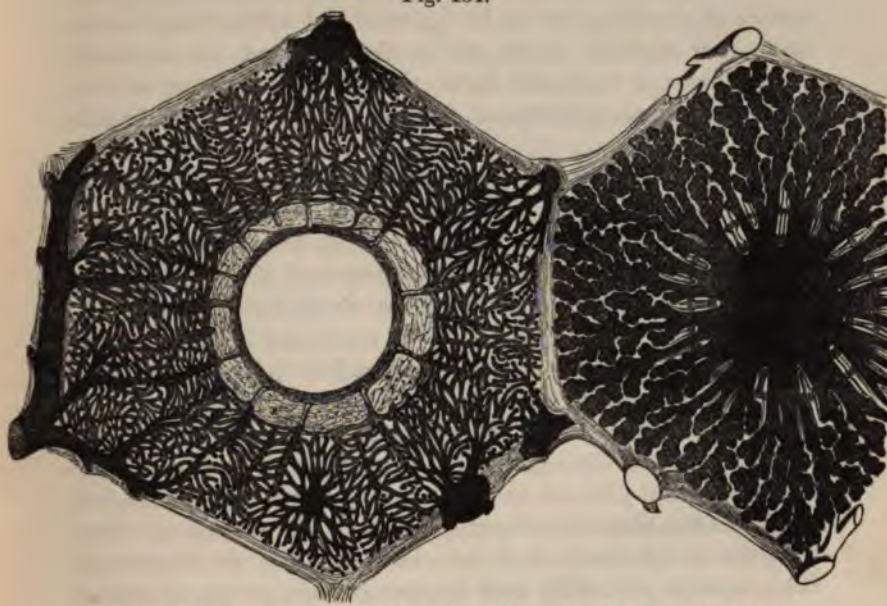

Fig. 134. Section of two pulmonary pipes or canals from the Goose. The air cavities of that on the right side tensely filled with dark-coloured injection. In that on the left the pulmonary vessels are injected.

are continuous with each other by transverse anastomoses, succeed each other at tolerably regular distances, and are connected by numerous longitudinal thin intermediate septa. A honeycombed surface is thus produced, the floor of which is formed by the parenchyma composing the voluminous wall of the air pipes. From the base of each of these alveoli several

passages are given off, which run at right angles, and in a radial direction from the longitudinal axis of the pipes. These are at first straight and simple, but soon branch in an arborescent manner, and indeed usually dichotomously at acute angles, till they terminate in small elongated cæcal processes (having a diameter of 0·015—0·009 of a millimeter in the Swan; of 0·010—0·006 in the Goose; and of 0·009—0·006 of a millimeter in the Pigeon), which, when strongly filled with injection, present numerous irregular lateral dilatations.

In the membranous wall of all bronchia extending to the surface of the lung, just as in the bronchial walls of the Mammalia, four separate layers can be distinguished: an external fibrous layer, a muscular layer, though this, perhaps, is not quite continuous, an internal fibrous layer, and an epithelial layer.

The *external fibrous layer* consists of fibrous connective tissue, chiefly running in a longitudinal direction, with fine elastic fibres distributed through it. A few thin cartilaginous laminæ occur at the commencement of the principal air passage, which embrace the tube for about two-thirds of its circumference. Small masses of fat are found scattered here and there in variable quantity, dependent probably on the condition of nutrition of the individual.

The *circular layer of smooth muscular fibres* lying on the inner side of the external fibrous layer, is not perfectly continuous, but presents narrow lacuniform spaces; beneath the cartilages the fibres are altogether absent. The septa projecting from the membranous wall into the lamina of the bronchial tubes contain, especially near the free borders, strong muscular bands, which communicate here and there with those that have been just described by delicate fasciculi.

The *internal fibrous layer* is composed of a rather thin layer of connective tissue, the fibres of which run longitudinally, and are intermingled with fine networks of elastic tissue. It presents at some points slight longitudinal ridges, and contributes in great measure to form the septa already described as arranged in a plexiform manner. It is invested on its inner free surface by a layer of *columnar and ciliated epithelial* cells, amongst which are numerous cup cells, and which be-

comes flatter towards the extremities of the bronchia. The nutrition of the membranous walls of these tubes is effected by means of a plexus of capillary vessels with elongated meshes, which is chiefly distributed in the internal fibrous layer.

Since from all those parts of the bronchia of the Bird that are immediately adjacent to the parenchyma of the lung the pulmonary canals are given off rectangularly and in close proximity, the bronchial wall must necessarily lose its membranous character, and become reduced to a trellis-work. The trabeculæ of this consist of compact bands of smooth muscular tissue intermingled with a few elastic fibres, lying in a matrix of fibrous connective tissue, which last expands to form the internal fibrous layer, supporting an abundant capillary plexus and a flattened columnar and ciliated epithelium. From these muscular trabeculæ surrounding the orifices of the pulmonary canals, finer fasciculi of a similar character are continued into the pipes themselves, and here form the thickened free borders of the above-mentioned transverse annular ridges, which, like the anastomosing and less strongly projecting longitudinal septa, are elsewhere composed of fibrous connective tissue and of delicate elastic fibres alone.

The matrix of the thick, spongy, external pulmonary-tube-walls is composed of a very delicately fibrous and quite homogeneous connective tissue with fine elastic plexuses, which supports the close capillary plexus destined to effect the interchange of gases in respiration.

This respiratory capillary system is developed from the branches of the pulmonary artery running to the extremity of the pulmonary canals, and passes from thence by minute terminal branches into the parenchyma, becoming ultimately continuous with the rootlets of the pulmonary vein, which pursue a similar but opposite course. The capillaries* that often slightly project into the lumen of the pulmonary canals, but are always closely invested by the matrix of connective tissue, or, in other words, are more or less completely imbedded in the

* Rainey maintained (*Medico-Chirurgical Transactions*, 1849, p. 50) that the capillaries projected freely into the lumen of the pulmonary canals without receiving support from any connective tissue.

wall, are of small size, and run transversely round the ultimate air passages, anastomosing frequently, and forming narrow longitudinally elongated meshes. I have not been able to demonstrate the existence of an epithelium covering them, though one is probably present.

Between the pulmonary canals there is a clear fibrous *interstitial connective tissue*, which in some birds, as the Goose and Duck, is of moderate thickness; whilst in others, as the Pigeon, it is scarcely appreciable.

The air-sacs of the Bird, which may be regarded as local projections of the bronchial wall, consist of fibrous connective tissue intermingled with delicate elastic fibres, and are traversed by a wide-meshed capillary plexus; on their inner surface they possess a simple pavement epithelium, the cells of which bear cilia only in the vicinity of the orifices.

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III. Structure of the Lung in Reptiles and Amphibia.

The lungs of Reptiles and Amphibia agree so closely in their structural relations, that they may here be considered together.

In the continuous series of forms presented by these animals in regard to the structure of their respiratory organs, the Tritons

and some Perennibranchiates, as the Proteus and Menobranchus, occupy the lowest grade, since in them each lung forms only a simple and internally smooth saccular expansion of the branch of air tube entering them. The remaining Amphibia present on the inner surface of their constantly saccular lungs, which hang from the bronchus like a berry upon its stalk, a plexiform series of ridge-like elevations, which however are not all of equal height, but project more or less into the cavity of the organ. The principal and for the most part quadrangular alveoli formed by the most strongly projecting ridges are subdivided into smaller depressions by less elevated septa, and these again by others, till ultimately a number of polygonal, and usually four or five angled, fossæ or alveoli are produced, the flat bases of which lie in contact with the investing membrane of the air sac, have lateral walls formed by these vertical ridges, and open directly into the general cavity of the pulmonary sac.

In the elongated tubular lungs of Ophidia and of Amphisbæna, the thick-walled anterior segment is characterized by the depth and complicated structure of the alveoli. The principal ridges, springing at right angles from the pulmonary wall, are not smooth-walled as in other Amphibia, but support secondary plexiform ridges on their surface, and thus alveoli are formed, the bases or fundi of which are no longer constituted by the proper wall of the lung, but by the principal ridges; whilst their orifices, instead of being directed towards the general cavity of the lung, open into the secondary cavities or alveoli bounded by these ridges or septa. In the lungs of the Snakes and Amphisbæna, the entire network of septa becomes more simple posteriorly, the ridges being less elevated, and ultimately vanishing so completely that the lung terminates in a smooth-walled and simple membranous sac.

Whilst the lungs of many Saurians (Anguis fragilis, Lacerta agilis, Scincus bistriatus) do not essentially differ in the structure of the air sacs from the simple lungs of Amphibia, in others, as for example the Chameleon, the common cavity of each lung presents two or more subdivisions, though not perhaps completely separated from each other, caused by the projection of one or several large septa which spring from the

wall of the pulmonary sac towards the bronchial orifice, and which, like other parts of the pulmonary wall, are themselves beset with smaller ridges circumscribing alveoli.

In the Chelonia such septa occur in greater numbers, traversing the whole cavity, and fusing completely with the tubular prolongation of the bronchus as it projects into this cavity; so that each lung is divided into a number of contiguous cæcal sacculi, usually arranged in two series, which no longer communicate with each other, but are accessible only through the prolongation of the bronchus.

The alveolar parenchyma covering the inner walls of these several segments of the lung exhibits a similar but rather more complicated structure than in Snakes. As in them, the main septa are here also not smooth-walled, but support on their lateral surfaces smaller septa arranged in a plexiform manner; these again have others, and so on.

Finally, in the Crocodile, by a still further development and complication of the alveolar parenchyma in the same direction, the above-described sac-like main air passages become constricted into the form of rounded tubuli, without, however, the actual formation of true solid-walled bronchia, such as are found in Mammals.

Throughout the Reptilia and Amphibia the histological matrix of the whole pulmonary tissue consists of fibrous connective tissue intermingled with a plexus of fine elastic fibres, containing in many instances, as in Salamandra maculata and numerous frogs, a large quantity of pigment cells filled with black granular material. In some animals, however, as the Chameleon, Scincus, Testudo græca, Emys europæus, and Coluber natrix, but few pigment cells are present, whilst in others, as the Lacerta agilis and Alligator sclerops, they are altogether absent.

The continuation of the bronchus penetrating to a greater or less depth into the lung, and forming either a partially grooved tube, as in Ophidia, or a straight tube perforated with rounded openings, as in Chelonia, or a ramified tube, as in Crocodiles, presents in its otherwise fibrous wall, rings composed of hyaline cartilage, homogeneous in structure, and frequently connected by communicating laminæ, the opposite sharp borders of which are united by a tense web of longitudinal elastic fibres.

In the fibrous stroma of the remaining parenchyma of the lung, smooth muscular tissue is found, and frequently in such abundance that it constitutes the greater portion of the whole tissue. A thin layer of circular muscular fibres is found even in the simple lung sacs of Tritons,* whilst in all lungs containing alveoli, compact muscular fasciculi occur as the principal supports of the alveolar meshes, and of the septa, being especially well developed at their thickened inner or free borders. From these strong and compact principal bundles thinner fasciculi are given off, and from these again a few isolated muscular fibres are distributed on the flat base of the alveoli near the internal surface.

The nerves distributed to the lungs of Reptiles and Amphibia, consisting of medullated and of non-medullated fibres, present here and there small collections of ganglionic cells, which were first closely examined by J. Arnold† in the lungs of the Frog, and were described by him as bell-shaped cells with granular contents, on the concave surface of which a straight dark-edged nerve fibre enters, the axis-cylinder of which terminates in the nucleoli. According to Arnold, fine processes are given off from the latter, running in a radial direction through the nucleus, and continuous with a number of fine fibres that traverse the granular contents of the cell, and ultimately enter the so-called spiral fibre which forms a series of spiral coils round the straight fibre.

A capillary plexus, which lies flat on the alveolar walls, is formed from the arterial trunks conveying venous blood to the lungs; its irregularly shaped rounded meshes do not exceed in diameter the capillaries, which themselves correspond in different animals with the size of the blood-corpuscles. This respiratory capillary plexus is distributed continuously over the lower alveolar septa, whilst upon the summits of all the higher ridges,

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* From my own observations I am able to substantiate the statements of H. Müller (*Würzburgen naturwiss. Zeitschrift*, Band ii., p. 131), in opposition to those of Reichert and Leydig, to the effect that a thin layer of circular muscular fibres is present in the Triton tœniatus.

† Virchow's *Archiv*, Band xxxviii., p. 431, 1863. *Centralblatt für die medicin. Wissenschaft.*, 1864, No. 42. Virchow's *Archiv*, Band xxxii., 1864.

as well as on the inner surface of the tubular continuations of the bronchia, and in the posterior segment of the lungs of Amphisbæna and Ophidia, it becomes continuous with a wide-meshed system of capillaries that are probably subservient to nutrition.

Fig. 135.

Fig. 135. Part of a pulmonary alveolus from the Frog (Rana temporaria). The left side is represented destitute of epithelium. Magnified 200 diameters. *a a*, Ends of capillaries; *b*, a heap of small columnar epithelial cells.

All respiratory capillaries are attached to the alveolar wall by one side only of their circumference, and thus lie with the greater part of their surface freely exposed in the air cavity of the alveolus, except where they are invested by a *continuous layer of tesselated epithelial cells.*

Fig. 136.

Fig. 136. Optical section of an alveolar wall from the edible Frog (Rana esculenta), after being hardened in perosmic acid. Magnified 320 diameters. *a a a*, Lumina of capillary vessels; *b*, nucleated columnar epithelial cells; *c*, muscular fibres of the alveolar wall.

The large polygonal cells of this alveolar epithelium are in

immediate contact with each other, laterally cover that surface of the capillaries which is turned towards the cavity of the air passage with a thin transparent laminar expansion, and send conical processes, usually consisting of the cell nucleus, with a little surrounding granular protoplasm, into the capillary meshes, to so great a depth, indeed, that they reach to the connective-tissue stroma of the alveolar wall, and thus completely fill the spaces of the capillary plexus.

These tap-shaped prolongations proceeding from the nucleus and granular protoplasm of each epithelial cell, are usually found at the angles of the cells, so that several cones may lie in juxtaposition, and occupy *one* capillary mesh. Still many cells occur, whose nucleated process is attached nearer to their centre, and with it completely fill a single capillary mesh.* Whilst now the respiratory surfaces of the lungs in Reptiles and Amphibia are lined by similar pavement epithelial cells,† the free borders of all the more prominent septa and ridges, as well as the internal surface of the bronchial continuation, are covered in general by a somewhat flattened columnar ciliated epithelium, in some parts of which numerous cup-shaped cells are distributed. The entire surface of the posterior non-respiratory segment of the lungs of the Snake and Amphisbæna is lined by a single but continuous layer of small polygonal, slightly granular pavement epithelial cells.

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* Whilst the results of my investigations in regard to the pulmonary epithelium of the Amphibia agree in all essential points with those of Elenz and C. Schmidt, I differ from these observers in one point relating to the alveolar epithelium of the reptilian lungs, as I found all the epithelial cells, however flat they might be, contain nuclei, whilst I was unable to discover any structureless non-nucleated plates. On filling the lungs with Müller's solution, and immersing them in it at the same time, the epithelium investing the respiratory cavities of Amphibia is not only rendered perfectly distinct, with all the cell contour lines, but this layer is wholly or partially raised and broken up into its constituent cells.

† We meet also here and there, especially in the lungs of the Frog, amongst the epithelium of the alveoli, with rounded groups varying from ten to thirty in number, of more cylindrical cells, which collectively fill a large capillary mesh, and appear to be to some extent subservient to the performance of a similar secretory function to that of the cup cells (fig. 135 *b*).

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IV. THE LUNGS AND SWIMMING-BLADDER OF FISHES.

The lungs of the Dipnoi, which anteriorly coalesce to form a common cavity, but posteriorly are free and sacciform, possess on their internal surface a system of anastomosing projecting laminæ, enclosing polygonal areas or alveolar-like spaces, which, like those of the lung of the Snake, become more complicated in front, in consequence of the formation of secondary alveoli on the walls of the principal air cells, whilst posteriorly they are merely arranged vertically on the general wall of the air sac, and thus open directly into the common air cavity. The more minute structural relations of the lungs of the Lepidosiren do not differ essentially from those already described in the lungs of Amphibia. The matrix here also consists of fibrous connective tissue, with large stellate pigment cells. The ridges projecting inwards contain dense bands of smooth muscular tissue which are particularly well marked at their free borders, increasing usually in extent with the height of the septa. A respiratory capillary plexus is distributed over the inner surface of the alveolar walls and the less prominent septa, the rounded

meshes of which scarcely exceed the diameter of the capillaries themselves. These are covered by a single layer of large flat epithelial cells, from which, as in Amphibia and Reptiles, short nucleated processes are given off into the capillary meshes.

The swimming-bladder of Fishes, notwithstanding that it is a pure hydrostatic apparatus, destitute of any respiratory capillaries, closely approximates the lungs in a morphological point of view.

The microscopic characters of the tissues entering into its composition are as various as the appearances it presents to the unaided eye, being sometimes simple, sometimes divided by constrictions or possessing diverticula, sometimes having walls that are perfectly smooth, and in other cases again with septa and ridges projecting from the inner surface. The principal constituent is an *external layer* of compact connective tissue, lying immediately beneath the peritoneum, composed of long, fine, and in many osseous fishes, peculiarly stiff connective-tissue fibrils that sometimes run collectively in the same transverse or oblique direction, and sometimes form decussating fasciculi, being then frequently arranged in two completely distinct layers, an external longitudinal and an internal transverse.

A process of ossification sometimes occurs in this external fibrous layer, as in Cobitis fossilis, Acanthopsis and Ophidium imberbe; in Cobitis assuming the form of a continuous trellis-work with rounded meshes.

The loose stroma of fibrillar connective tissue, which may be regarded as the *internal layer*, frequently contains elastic lamellæ lying parallel to the surface. In the greater number of osseous fishes these are remarkably delicate; in a few, however, and especially in the anterior part of the swimming bladder of the Cyprinoid, they acquire the character of a dense fenestrated membrane. Peculiar elongated, four-sided, delicate elastic leaflets frequently appear between the elastic lamellæ; as, for example, in Esox lucius, Perca fluviatilis, Gadus callarias, Gadus zota, etc., which are perfectly transparent and structureless up to the oval nucleus, usually situated near the middle, and when isolated roll up like a leaf. These leaflets usually lie superimposed on each other in small packets, but can be

easily detached. The thick map-like layer of the swimming-bladder of the sturgeon presents quite a peculiar connective-tissue formation; for, putting aside a sparing quantity of loose fibrillar stroma, it is entirely composed of relatively short fusiform and flattened fibres, which, on the one hand, unite to form larger bands, and on the other can be broken up into smaller elements, presenting similar characters. In addition to small, short, dark, longitudinal striæ, which may be regarded as the indications of connective-tissue corpuscles, no structure can be distinguished in these highly refractile and, as I here particularly desire to state, strongly doubly refracting elements.* On boiling, and after treatment with acids, they swell up to an extraordinary extent, and quickly dissolving form gelatine.

Muscular tissue, sometimes of the striated, and sometimes of the smooth form, is associated with the connective-tissue matrix of the swimming-bladder in very various modes. The swimming-bladder of Polypterus bichir and Amia is invested immediately beneath the peritoneum by a sheath consisting of two superimposed and decussating layers of transversely striated muscular tissue. In the latter each layer is composed of only a single layer of fibres, but in Polypterus there are a considerable number of layers in each. In a third Ganoid, Lepidosteus osseus, bands of transversely striated muscular fibres, which either anastomose with one another directly or through the intermediation of tendinous cords into a plexus, lie, not on the external surface of the swimming-bladder, but in the here largely developed membranous septa and trabeculæ that surround the alveoli of the *internal* surface. In the sturgeon, on the other hand, there is a continuous layer of *smooth* muscular tissue in the *external* fibrous layer. A few osseous fishes, as, for example, Trigla, Dactyloptera, and Zeus, possess sharply defined plates or bands of transversely striated muscular tissue, situated on certain parts only of the external surface of the swimming-bladder, others, as the Cyprinoids, have in the middle line of the anterior portion of the *internal* layer, and on its inferior aspect, a longitudinal band of transversely

* The optic axis corresponds to the longitudinal axis of the fibres, which, like muscular fibres, are *positively* doubly refracting.

arranged smooth muscular fibres, which, near the point of constriction of the sac, expand into a complete annulus; whilst in the posterior segment of the sac two longitudinal bands of smooth muscle with transverse fibres are present, lying in the most external part of the most external layer. Other fishes again, as, for example, Esox lucius, Gadus callarias, and Perca fluviatilis, exhibit a continuous thin layer of smooth muscular fibres in the *internal* layer.* Lastly, the musculature may be altogether absent, as in Cobitis and others.

In some fishes, as Accipenser and Salmo, the vessels springing from the aortic system, and consequently conveying arterial blood to the swimming-bladder, break up into a wide-meshed capillary plexus ministering to the nutrition of the organ, from whence the blood passes into systemic veins; in many others, however, peculiar vascular arrangements are found in the external part of the internal layer, which were first carefully examined by Joh. Müller, and referred by him

Fig. 137.

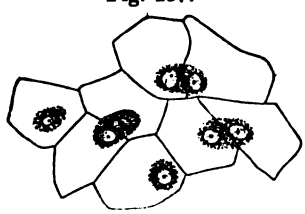

Fig. 137. Epithelium detached from the internal surface of an alveolus of Testudo græca. Magnified 200 diameters.

to the category of retia mirabilia. In these instances arteries suddenly break up into sometimes expanded, sometimes more restricted, brushes or tufts of vessels, from which tree-like plexuses of capillaries originate either immediately or after the formation of a few larger vessels. From these plexuses of capillaries distributed upon the internal surface of the swimming-bladder, venous retia mirabilia take origin (either directly or after the formation of a few large veins), which are

* Leydig describes a layer of smooth muscular fibres in the external layer of Esox, but I have not been able to discover it.

so intercalated between the arterial retia that a transverse section of the entire mass exhibits arterial and venous tubules in tolerably equal amount, and in close juxta-position.

The continuous epithelial investment that lines the internal surface of every swimming-bladder, is composed in the Sturgeon, and, according to Leydig, in Polypterus bichir also, of columnar ciliated cells; in the osseous fishes, on the other hand, there is a single layer of tesselated epithelial cells, which differ from those covering the capillary plexuses arising from the arterial retia, in being less flattened or more cubical, in possessing cloudy granular contents, and consequently in presenting the appearance of gland cells. Their glandular function is rendered still more probable by the circumstance that they completely line, as a kind of glandular epithelium, the lacuniform or purse-like inflections of the capillary bodies.

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CHAPTER XXI.

THE KIDNEYS.

By C. LUDWIG.

On dividing the fresh kidney of a Mammal from the papillæ to the fibrous capsule, we may discern even with the naked eye a distinction in the exposed surface between the striated medullary portion and the granular cortex. These two segments are concentrically arranged. If the blood and urinary vessels of the organ be injected with differently coloured fluids, they may be observed to pursue a radial direction, both in the medulla and in the cortex.

On the exposed surface of the medulla, striæ radiate from the papillæ towards the cortex, which are coloured by the fluid injected into the urinary tubules.

These striæ are in immediate contact at and a little above the papillæ, so that up to this point the medulla presents a uniform tint, and the term *papillary region* has been applied to it. As the striæ recede from the papillæ, they separate from each other, so that previously to their entrance into the cortical layer they run with intervals of about their own diameter. The intervening spaces are occupied by vessels presenting the colour of the fluid that has been injected into the bloodvessels. That portion of the medulla in which the urinary and blood vessels alternate with one another is termed the *limiting* or *marginal layer* of the medulla. In the cortex striæ also occur, which, both from the kind and intensity of their colour, as well as from their direction, evidently constitute the immediate prolongations of those striæ of the medulla

formed by the urinary tubes. Such striæ emerging from the medulla, and running to almost the extreme circumference of the cortex, are termed *medullary rays* (processes of the pyramids). The remaining portion of the cortex, excluding these,

Fig. 138.

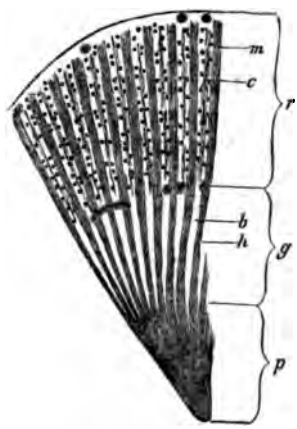

Fig. 138. Horizontal section of the kidney of a Dog, in which both the urinary and blood vessels have been injected. *p*, Papillary region ; *g*, marginal region of the medulla ; *r*, cortex. The dark striæ of the medulla (*h*) represent fasciculi of urinary tubules, and they are continued as medullary rays (*m*) in the cortex. The transparent intervening portions of the medulla (*b*) correspond in position to the fasciculi of bloodvessels of the intermediate layer. The transparent portion of the cortex, beset with dots (glomeruli, *c*), indicates the labyrinth.

chiefly presents the tint of the injection thrown into the bloodvessels; and this part may be termed the *renal labyrinth* (or cortex, in the more restricted sense of the word).

The application of the microscope to the differently coloured portions shows that each is composed of a great number of canals, which are partly continuous with the bloodvessels, and partly with the urinary passages. These two kinds of vessels form by far the largest part of the substance of the kidney.

Urinary Tubules.

1. Course and Diameter.—In consequence of their frequent change of direction, the tubuli uriniferi pursue a relatively long course in the substance of the kidney; and in one part they may be seen to be isolated, whilst in another they coalesce with others to form common trunks. At certain points their diameter varies to a considerable extent.

Every tubulus uriniferus commences in the labyrinth by means of a spheroidal enlargement, which constitutes the capsule of a renal corpuscle or glomerulus. This is continuous by a constricted portion—the neck of the capsule—with a wide tube that runs with manifold windings towards the medulla; on reaching the margin of the medullary portion the tortuous and wide tubule suddenly becomes attenuated, and runs as a fine and straight canal to a variable distance into the medulla (forming the descending or closed limb of the loop), where it forms a narrow loop termed Henle's loop, returning again towards the cortex by a similar straight canal (the ascending or open limb of the loop). The recurrent limb of the loop does not return exactly to the point from which the opposite limb commenced, but as it were avoids the labyrinth, and applies itself closely to the nearest medullary ray. Sooner or later, however, it leaves this straight course, and makes numerous angular windings, constituting the so-called intermediary portion between the sinuous canals of the labyrinth. From thence it returns, after forming an arch, the convexity of which is directed towards the surface of the kidney, to the medullary ray, where its independent course terminates. The mode in which this occurs is that several canals running from various quarters to the same point coalesce to form one of the straight and wide collecting tubules.

Before we follow this last any further, the numerous variations in diameter that the tubules experience from their first emergence from the cortex to their final return to the medullary ray or to their junction with the collecting tubes must be noticed. It has already been stated that the canal, where it ceases to be tortuous, and extends towards the loop of Henle, undergoes considerable attenuation. The distance that it

remains narrowed is not in all instances the same. It frequently preserves its smaller diameter throughout the descending limb of the loop, but just as often assumes a wider diameter

Fig. 139.

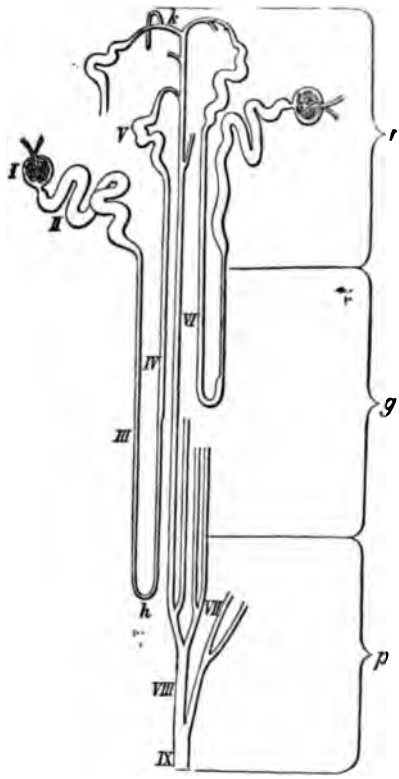

Fig. 139. Diagrammatic representation of the course of a urinary tubule from the human kidney. *p*, Papillary layer or region ; *g*, marginal layer of the medulla ; *r*, cortex ; I, capsule of the glomerulus, which is continuous by its neck with the tortuous portion of the canal (II). This becomes attenuated at the contiguous borders of the medullary and cortical portions of the kidney, and forms the descending limb of the loop (III), then constitutes Henle's loop (*h*), and continues as the ascending limb of the loop (IV). This passes into the intermediary portion (V), which, by an externally convex arch, enters the apex of the collecting tubule (VI). This last unites with others in the same medullary ray (VII) to form a principal tubule (VIII), and this last with other tubules to form a papillary duct (IX).

immediately before it forms the loop, though it is here always materially smaller than in the tortuous portion of the canal. This alteration in diameter continues unaltered to near the point where the canal becomes continuous with the intermediary portion, on arriving at which it usually becomes slightly narrowed. This, however, is but temporary, and it speedily enlarges again, in the windings of this intermediary portion, to nearly the same diameter that it presented in its tortuous portion. In some few kidneys this dilated part of the intermediary portion offers the remarkable appearance of its hitherto cylindrical calibre, presenting irregular dilatations varying in number and size. In the final curve, by which the intermediary portion joins the collecting tube, the canal once more becomes temporarily narrowed.

In its course as an isolated tube the canal is thus seen to change its diameter no less than seven times; viz., 1. The constriction at the neck of the capsule; 2. The dilatation extending from the neck of the capsule through the tortuous portion; 3. Constriction as it extends towards the loop of Henle; 4. Dilatation occurring in the open or ascending limb of the loop; 5. Constriction where it becomes continuous with the windings of the intermediary portion; 6. Dilatation in these latter; and lastly, 7. Constriction in the portion that extends from the intermediary portion towards the collecting tubes.

We now revert to the consideration of the collecting tube. This, as has already been mentioned, is formed at the cortical extremity of a medullary ray, by the junction of several canals previously running separately into a common trunk, just as the branches of a tree spring from, or are united into, one stem.

After the collecting tube has been once formed, it still continues to receive a few branches just below the crown, and from thence runs separately, and in a straight direction, to the papillary portion of the medulla; it consequently always remains in the line of a medullary ray. When the several collecting tubes have reached the papillary region, they gradually coalesce, until at length only a few of the originally very numerous tubes remain. In every instance two vessels only join together. In this way all the collecting tubes of one medullary ray coalesce into a few chief tubes, and then the

chief tubes of different medullary rays begin to coalesce, and so on. The ultimate passages resulting from this paired mode of union—the so-called ductus papillares—open ultimately on the free surface of the papillæ. As regards the diameter of these canals, the general rule is, that every tubule resulting from the junction of two is slightly wider than those which coalesce to form it.

2. COMBINATION OF THE TUBULES TO FORM PRIMITIVE CONES. —A limited number of tubuli uriniferi stand in a more intimate relation to each other than to any of the others. The association of these is effected by the circumstance that the collecting tubes of these groups run in one and the same medullary ray, and ultimately open into one and the same chief tube. The tubules that form the collecting tubes, however, even when they run separately, are so arranged that they are easily recognized as belonging to the same group. All the portions which belong to such a division preserve, when regarded as a whole, somewhat of the appearance of a cone or of a flask, the apex of which is in the papilla, and the base in the cortex. As the kidneys, so far as regards the tubuli uriniferi, are composed of an aggregate of many such primitive cones, as they may be called, it is necessary in order to understand the kidney to know their structure. In describing them we shall commence from the papillary extremity of the tubuli uriniferi, and pass towards the cortex.

Each of the main or principal tubes, by the coalescence of which the papillary ducts are formed, passes from within or from just above the papilla to the middle of each medullary ray, and having reached that point, speedily undergoes dichotomous division into a number of branches: as far as we know, this division occurs within a limited region of the medulla, so that each collecting tube becomes independent at a short distance above the papilla. The collecting tubes proceeding from each principal tubule run all together in close approximation, and nearly parallel to one another, as far as to the periphery of the kidney, and form the stem of the fasciculus of tubules to which the term "medullary ray" has been applied. Each collecting tube remains unbranched until it has nearly arrived at

the cortical extremity of the medullary ray. It here divides into a number of branches of nearly equal size, each of which, remaining isolated to its extremity, forms a urinary tubule.

Each of these tubuli uriniferi proceeds in the form of a short arch from the collecting tube, and with its intermediary portion winds at the base of the cone, as far as to the surface of the kidney, so that in penetrating from the fibrous capsule into the substance of the organ we first meet with tortuous canals, which chiefly consist of the windings of the intermediary portion. From this point the windings return again to the axis of the cone (medullary ray), and, pursuing a straight course, enter the spaces between the collecting tubes of the medullary ray. Wherever in the course of this path the canaliculi reach the medulla, the formation of the loops begins, so that throughout the entire limiting or peripherical layer of the medulla tubule after tubule loops in the manner described. After having formed the loop, the ascending limb of each, as it passes on towards the tortuous portion, still continues to lie in juxta-position with its own fasciculus of collecting tubes, but gradually separates from them, and forms the tortuous portion. These last finally form a ring around the medullary ray in the cortex, where this is not already invested as by a sheath with the windings of the intermediary portion.

3. Coalition of the Primitive Cones to form the Pyramids or Renculi.—If the mode in which the main canals of the primitive cones in the papilla coalesce to form the ductus papillares be understood, the formation of a pyramid from the association of numerous primitive cones will also be intelligible. Two points only require special notice. The first relates to the mode of origin of the lacuniform spaces of the limiting layer of the medulla that are filled with blood-vessels. These result from the circumstance that at the point where the cortex ceases the medullary ray also suddenly loses its sheath of cortical substance which has hitherto invested it. The investment of the primitive cone thus forms there a deep inflection like that of a flask, at the part where the belly is continuous with the neck. If we now consider two or several such flask-like bodies to be so arranged that their bellies and

the free extremities of their necks are in contact, a space must necessarily intervene where the belly is continuous with the neck.

The other point relates to the mode of coalescence of the collecting and chief tubules to form the ductus papillares, which occasions the rounded truncated form of the papilla. The mode in which this is effected may be easily understood

Fig. 140.

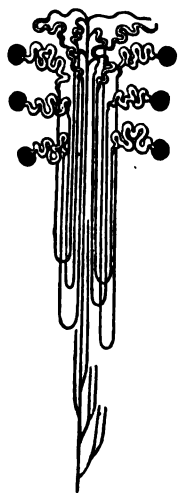

Fig. 141.

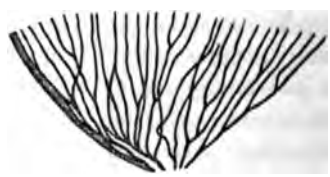

Fig. 140. Diagrammatic representation of the mode in which the tubuli uriniferi are arranged to form a primitive cone.

Fig. 141. Coalescence of the tubuli uriniferi in the papilla. Diagrammatic representation.

from the accompanying drawing (fig. 141) of a longitudinal section through a papilla. It is here seen that the tubules run from all sides, in a more or less curved manner, to reach the few and short papillary ducts.

STRUCTURE OF THE WALL OF THE URINARY TUBULES.—As often as the tubuli uriniferi change their diameter and direction, they also become altered in structure.

The lamina of which the spherical capsule consists, so far as it can be broken up, consists exclusively of a mosaic of cells closely resembling those composing the wall of the blood and lymphatic capillaries; on their outer surface is a little connective

tissue, which is especially abundant around those capsules which lie next the medulla.

The glomerulus of vessels contained within the capsule also

Fig. 142.

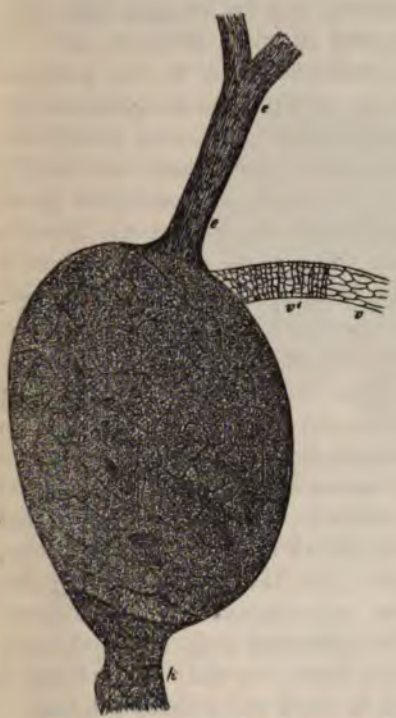

Fig. 143.

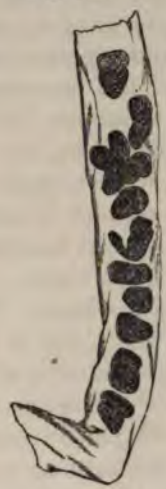

Fig. 144.

Fig. 142. Capsule of a glomerulus from the kidney of a Rabbit, after being subjected to the action of nitrate of silver and carmine. The endothelial cells of the wall of the capsule (*a*) in part contain oval nuclei (*a'*). The endothelium is continued into the neck (*h*). The vas afferens (*v*) presents at *v'* silvered lines, which indicate the circular muscles, and at *v* the markings of the endothelium. *e*, The vas efferens. The silvered lines show that its epithelial cells are fusiform.

Fig. 143. Tunica propria of a tortuous canal. The interior contains detached masses of epithelium.

Fig. 144. An isolated fragment of a tortuous canal still containing epithelium. Moistened with very dilute hydrochloric acid.

obtains an investment that adheres closely to the vessels, and of which we shall hereafter speak more at large.

From the neck of the capsule to the commencement of the ductus papillares, the wall of the tubuli uriniferi is composed of a basement membrane (tunica propria), the inner surface of which is lined by an epithelium. In general the basement membrane appears to be homogeneous, and cannot be further divided, but occasionally a nucleus can be brought into view in its substance by carmine; and in some instances, and for short distances, the same appearances occur in the tortuous canals, when treated with nitrate of silver, as are presented by the blood and lymph capillaries under the same conditions. The basement membrane is as clear as glass, elastic, and readily swells up in water. It can be very easily demonstrated in an isolated condition. The epithelium lining the capsule forms a single layer, and is nucleated. The shape of the nucleus is usually the same in all instances; being spherical, sharply defined, and with numerous granules scattered through its substance. The cells, on the contrary, present various modifications.

In the tortuous portions of the canals the nuclei, standing at tolerably equal distances from each other, are imbedded in a pulpy mass. The latter presents numerous fissures that are particularly obvious in every tranverse section when a coloured injection thrown into the urinary tubules has penetrated them. These fissures, however, lie at very irregular distances, and in brief it would appear that the mass investing the nuclei, and to be regarded as cell-substance, is not differentiated into separate cells. The epithelial pulp is only loosely attached to the basement membrane; so that when fresh it can be easily forced out of the isolated and divided tubules.

How far the epithelial mass projects into the canal depends upon the distension of the latter. If this, owing to an artificial arrest of the discharge of the urine, be considerable, the epithelium lining the canal is flatter; on the other hand, if the kidneys have been empty before death, the epithelial ring appears thicker. The pulpy investment consequently adheres firmly to the basement membrane, and follows its alterations of form.

The material of which the pulpy bodies of the cells is com-

posed is by no means homogeneous, but presents numerous fat drops and other dark granules distributed through its amorphous substance, that clear away on the addition of diluted acids. These particles occasion a degree of cloudiness that is usually sufficient to conceal the nucleus, unless acid have been previously applied; and this peculiarity has led to the term cloudy epithelium being applied to indicate that which lines the tortuous urinary tubules.

Fig. 145.

Fig. 146.

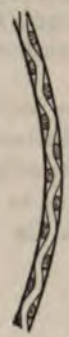

Fig. 145. Section through the cortical canals of a fresh kidney, showing the cloudy epithelial layer. The spheroidal nuclei are concealed; in the wider tubules, irregular, in the narrower regular, fissures divide the epithelial mass.

Fig. 146. An isolated fragment of a small urinary tubule, with fine, clear, delicate epithelium, and with alternate swellings caused by the nuclei.

The slender portions of the canal (fig. 146) which run to and from the loop of Henle, instead of being lined with this dark and thick epithelium, possess a thin and clear continuous layer which projects considerably at certain points, owing to the presence of nuclei.

Where on the other side of the loop the diameter of the tubule again increases, the shape of the investing mass of the nucleus is so far altered and peculiar, that a split now begins to make its appearance about half-way between every two nuclei, which is open towards the wall, and pointed towards the bore of the canal. The epithelium in consequence presents the appearance of being composed of clear separate columnar cells,

which in proceeding from the medulla towards the cortex are arranged in an imbricated manner.

In the windings of the intermediary portion the epithelial lining reassumes the pulpy character it presented in the

Fig. 147.

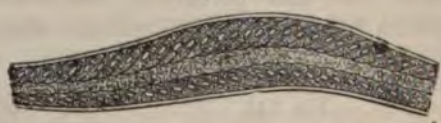

Fig. 147. From an ascending limb of a loop of Henle, to show the imbricated arrangement of the epithelium.

tortuous portion of the tubule. In the collecting tubes, as far as the ductus papillares, the epithelium is composed of isolated and distinctly defined columnar cells, the broader base of which is applied to the wall of the canal, and their truncated apices towards its lumen. Finally, in the ductus papillares the

Fig. 148.

Fig. 148. Transverse section through the fresh medullary portion of a kidney, to show the characters of the epithelium in the tubuli uriniferi. The dark circles (*b*) are sections of bloodvessels. The epithelium is quite transparent, so that the spheroidal form of the nuclei is clearly visible. R, Collecting tubes, in which the epithelial cells are completely individualised; *s*, slender and wide limbs of the loop. Between the tubules is a mass of striated connective tissue.

tubules lose their basement membrane, so that the wall is here formed of the epithelium alone, just as occurs in the ducts of the sweat glands where they perforate the epidermis.

As the tubuli uriniferi of all Mammals present a general accordance, in their structure, course, and relations, with the above description, the kidneys of the different classes would assimilate in the closest manner, were the transverse and longitudinal proportions of the canals similar. The only difference that could then exist would be in the number of the canals participating in the formation of the organ. This, however, it is well known, is not the case. The obvious differences which exist between the kidneys of different Mammals show that in the several classes, in reference to the proportions of the primary urinary passages, a great field of variation exists.

Fig. 149*.

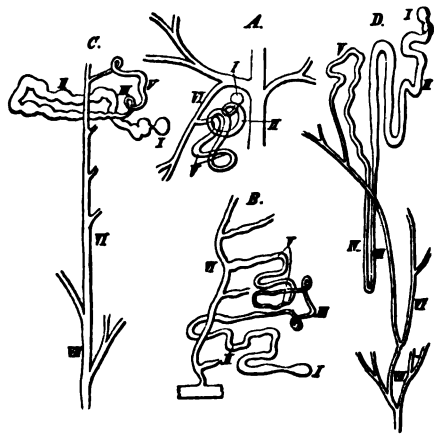

Fig. 149*. Varieties of urinary tubules. (All these figures have been taken from Hüfner's work.)

The most superficial examination of preparations obtained by section or by breaking up the tissue of the organ, shows that not only the absolute length and thickness of the kidneys vary in different specimens, but that a similar variation exists in the length of the different segments of the canals. Apart from all other evidence, this is sufficiently proved by the unequal proportion presented by different kidneys in the amount of the cortical and medullary proportions of their substance. It will be impossible to arrive at any very precise conclusion in regard to this undoubtedly important functional relation of the cor-

tical to the medullary portions of the kidney until means have been discovered rendering it more easy than at present to isolate the tubuli uriniferi, and to obtain them in a less broken condition.

From the statements that have been made upon the anatomy of the tubuli uriniferi in other vertebrate classes the following excerpts may be made.

The diagrammatic outline (fig. 149 D) is taken from the kidney of the Pigeon, and the remarkable agreement it presents with the urinary canals of the Mammal is deserving of notice. The several subdivisions of the tube distinguishable in the latter are seen to recur there, and the epithelial covering preserves the same features in both. As far as our present knowledge goes it would appear that the tubuli uriniferi in all Birds resemble those of the Pigeon.

Fig. 149 C represents the course of the urinary tubules in the kidney of Testudo. We see here the capsule with its neck (I), the dilated tortuous portion (II), the narrowed portion with which this is continuous (III), and lastly the dilatation (V), immediately preceding the formation of the collecting tube. The only differences existing between this and the type found in Mammals are that the tortuous portion of the tube is not smooth in Reptiles, but presents a nodulated surface, and that the constricted portion lying between it and the intermediary portion is of a different shape than the loop of Mammals. The epithelium in the neck of the capsule in the Tortoise is but little elevated, whilst it is high and sometimes pigmented in the tortuous portion, and flat and transparent again in the narrowed portion.

Fig. 149 B shows the course pursued by the tubuli uriniferi in the Frog. The elongated capsule is continuous by its protracted neck (I) with the tortuous tube (II). This becomes attenuated at III, and, again undergoing gradual dilatation, forms a second very tortuous portion (V), which discharges its contents into the collecting tube. The wall of the capsule is invested by a strong layer of connective tissue, and the epithelium lining it is low, clear, and frequently ciliated. In segment II the epithelium is composed of tall polygonal cells, in III the cells are transparent and low, and lastly, in the segment analogous to the intermediary portion they are tall and cloudy.

The urinary tubules of the Triton closely resemble those of the Frog in their structure and course.

Fig. 149 A is a diagram representing the urinary tubules of the

Cobitis fossilis. The capsule is here relatively long, the neck very long, and the tortuous tube extends from the neck to the collecting tube, which is of large diameter at its commencement and termination, but in the middle of its course, and for a short distance, is considerably attenuated. The height of the epithelium varies with the diameter of the canal; it is everywhere transparent.

The simplest form of kidney with which we are at present acquainted is that of Bdellostoma Fosteri. The urinary tubules in this instance are composed of a capsule, the neck of which becomes continuous with a wide tube that after a short course opens into the collecting tube. Nothing is known in regard to the epithelium of this primitive form of kidney.

Bloodvessels.

The kidneys receive their chief supply of blood through the renal arteries, but occasionally they are partially supplied by the phrenic, lumbar, and suprarenals, very delicate branches of which anastomose with those of the renal artery on the fibrous capsule. Although the medulla, cortex, and capsule are thus supplied by a single trunk, the capillaries and ultimate arterial divisions are separable into three parts, corresponding to these several portions of the kidney.

Bloodvessels of the Cortex.—The renal arteries send by far the greatest part of their blood through the cortex, and the trunks, without the formation of plexuses, undergo division so rapidly that very shortly after their entrance into the cortex they have broken up into very fine arteries, the arteriolæ interlobulares.

In longitudinal sections of the kidney these vessels are seen occupying the interspace between two adjoining medullary rays, and also where several primitive cones are in contact with each other. By far the greatest part of these branches, as soon as the medullary rays cease, becomes indistinguishable to the naked eye, though a small portion penetrates to the most superficial layer of the cortex, and reaches the fibrous capsule. Every arteria interlobularis, in its course between the tortuous tubules, gives off branches in quick succession, and so that small trunklets extend to the dilated extremity of a

tortuous canal (capsula glomeruli). Taken collectively, therefore, the arteriæ interlobulares give off at least as many branches into the cortex as there are beginnings of urinary tubules in it; it is very probable also that they do not exceed this number.

Each of these terminal arterial branches (vas afferens glomeruli) runs straight from its origin to the nearest terminal dilatation of a urinary tubule. A few of these very numerous vasa afferentia, before they reach the spherical extremity of the urinary tubule, give off a very fine branch, that immediately breaks up into capillaries, through which the blood passes into the capillary plexus investing the urinary tubules. Every vas afferens alike, whether it has previously given off branches, or remained undivided, runs to one of the spherical dilatations of the urinary tubule, and perforates the wall opposite to the commencement of the tortuous canal or neck. On reaching the interior it breaks up into a brush of free capillaries, called the glomerulus, which again within the capsule unite to form a venous trunk, the vas efferens glomeruli. This little vein, of about the same size as the vas afferens, runs in close proximity to the latter, and usually perforates the capsule at the same point.

Respecting the arrangement of the vessels within the glomerulus, the following facts only are known. The vas afferens divides immediately after its entrance into the spherical capsule into from four to eight branches, which, widely diverging, run towards the neck. In the same manner each branch ramifies, and these secondary twigs coalesce, as it would appear, gradually towards the centre of the capsule to form the vas efferens. Very frequently the capillaries proceeding from the primary branches of the arterial vas afferens reunite into a common veinlet, so that the vas efferens is recomposed in the same manner that the afferent trunk divided. When this occurs, the glomerulus presents several vascular lobules, which are continuous at either end with an artery and a vein. Although the glomerulus is never adherent to the membrane of the capsule, the walls of the capillaries are not in immediate contact with its fluid contents, a layer of not very well-defined cells with spherical nuclei investing their surface.

The exact relations of this investment are still very obscure. It is apparently stretched uniformly over each lobule of which

Fig. 150.

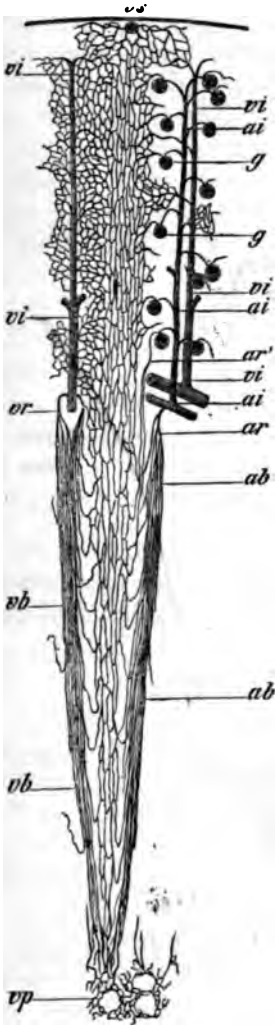

Fig. 150. Diagram of the circulation in the kidney. *a i*, Arteria interlobularis, sending numerous vasa afferentia to the glomeruli (*g*); the vas efferens proceeding from each of the latter run in the cortex, partly into the wide-meshed capillary network of the medullary rays, partly into the narrow-meshed plexus of the tortuous canals. From these plexuses the venæ stellatæ (*v s*) are formed at the surface of the cortex, and the venæ interlobulares (*v i*) in the labyrinth of the cortex. Into the medullary portion penetrate the arteriæ rectæ veræ (*a r*), proceeding from the renal arteries, and also the vasa efferentia of those glomeruli which are situated around the medulla. From the arterial fasciculus (*a b*), formed by the arteriæ rectæ, the capillaries destined for the urinary tubuli of the medulla take their origin. The blood circulating in these plexuses is returned by the venulæ rectæ, of which many run together to form a fasciculus with parallel striation, as at *v b*. The vessels of this fasciculus coalesce to form a venous trunk (*v r*), which empties itself into a large renal vein. A venous plexus (*v p*) surrounds the openings of the urinary tubules upon the papilla.

the glomerulus is composed, and consequently binds the several vessels together; on the other hand, it is not extended from

lobule to lobule, but if continuous at all, is only so at their roots.

We now return to the vas efferens glomeruli. When this

Fig. 151.

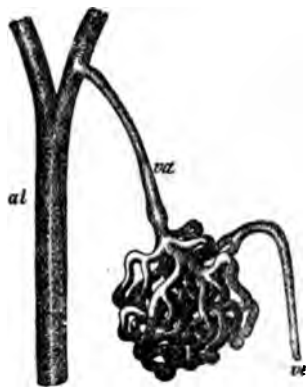

Fig. 151. Glomerulus from the kidney of the Cat. Magnified 300 diameters. *a i*, Arteria interlobularis; *v a*, vas afferens; *v e*, vas efferens.

has left the capsule, it runs towards the nearest medullary ray; or where this, as in the outermost layer of the cortex, is absent, immediately towards the tortuous portion of the tubules, where

Fig. 152.

Fig. 152. From the kidney of the Pig, showing the mode of division of a vas afferens into a lobulated glomerulus.

it divides into a number of speedily anastomosing capillaries. As, with the exception of those lying near the medulla, all the vasa efferentia divide in this manner, and as the marginal

vessels of all the groups of capillaries given off from the adjoining vasa efferentia communicate with each other, a continuous capillary plexus is formed, extending through the entire cortex. This plexus, however, does not, like the cortex itself, form a distinct layer; but is continuous, by means of the plexuses which surround the medullary rays, with the capillary system of the medulla.

The meshes of the cortical plexus distributed over the tortuous portion of the tubules are narrow, and more or less circular in form; those on the other hand which traverse the medullary ray are wider, and elongated in the direction of the course of the tubules. The capillaries composing this plexus are never

Fig. 153.

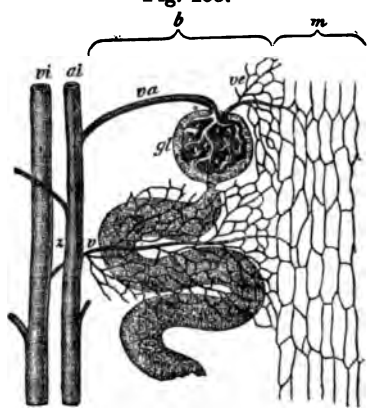

Fig. 153. Diagrammatic representation of the bloodvessels in the substance of the cortex of the kidney. *m*, Region of the medullary ray; *b*, region of the tortuous portion of the tubules; *a i*, arteria interlobularis; *v i*, vena interlobularis; *v a*, vas afferens glomeruli; *v e*, vas efferens glomeruli; *g l*, glomerulus; *v z*, venous twig of the interlobular vein.

adherent to the urinary tubules; lacuniform spaces, frequently filled with fluid, always intervening between the walls of the blood and urinary vessels.

From the capillaries just described, minute veins originate at small distances from each other, which quickly coalesce to form larger trunks. In the most external layers of the cortex, which contain no glomeruli, the coalesence of the smaller veins

occurs in a radial manner, forming the venæ stellatæ. The common trunk proceeding from the centre of a star runs into that portion of the cortical region which contains glomeruli and medullary rays, and there becomes applied to an arteria interlobularis. The several veins thus originating run towards the boundary of the medulla and cortex, receiving numerous and variously sized branches which originate in the capillaries of the cortical plexus. The veins are always so imbedded in the cortex, that even when empty their orifices remain open.

BLOODVESSELS OF THE MEDULLARY PORTION. — The blood flowing to the medullary portion of the kidney is, with but slight exception, conveyed by long vessels termed the *arteriæ rectæ*, which collectively enter the medulla from the side of the cortex (fig. 150, *a r* and *a r'*). The term arteries, in the fullest sense of the word, is only applicable to a portion of them; the remainder, indeed, transmit their blood into the capillaries of the medulla, but do not present either the structure of the walls or the mode of distribution of arterial vessels.

Those arteriolæ rectæ that from their structure and mode of origin are clearly arterial in character, proceed from the branches of the renal arteries, that also give off the arteriæ interlobulares towards the cortex. The other portion of the arteriolæ rectæ, that have no circular muscles in their wall, are nothing but the very elongated vasa efferentia of those glomeruli which are in immediate proximity to the medulla.

The whole of the arteriolæ rectæ, whatever may be their origin, immediately run towards the fissure-like spaces in the marginal portion of the medulla between the fasciculi of urinary tubules.

Many of the little trunklets, even before their entrance into these spaces, divide into several branches, and having reached them, continue to divide whilst pursuing their course towards the papillæ. In this manner a brush of parallel vessels arises from the trunk of each arteriola recta; and when the vessels of this brush come into contact with the converging bundles of the urinary tubules, they break up into capillaries that form looped plexuses around the tubules. And as, on account of the progressive narrowing of the fissure, one artery after another

thus reaches the fasciculus of tubules, so do they successively break up into capillaries. The number of the arteriolæ consequently diminishes towards the papillæ, until in the latter only one or two remain, which break up into capillaries, and are distributed over the papillæ themselves.

The capillary plexus investing the urinary tubules of the medulla is wide-meshed, and, as has been already mentioned, when it is in immediate contact with the cortex, is uninterruptedly continuous with the capillaries of this region of the cortex.

In consequence of this arrangement the supply of blood to the medullary portion is partially independent of that of the cortex, and the former would still continue to obtain its supply even if all the cortical vessels were obliterated; on the other hand, the medullary portion is to some extent dependent on the vascular supply of the cortex, since it receives at least a portion of the blood circulating through the vasa efferentia of those glomeruli from which the arteriolæ rectæ proceed. The blood issuing from the glomeruli does not, however, always pass through the medullary portion, since it not unfrequently happens that a vas efferens, before it gives off arteriolæ rectæ, supplies branches to the tortuous portions of the tubules that break up into capillaries in the same manner as in other parts of the cortex.

The veins of the medullary portion run in the same fissures as the arteries. The structure of their walls differs from that of other veins of the same size, in the circumstance that the cells of their endothelial lining are extraordinarily elongated in the direction of the axis of the vessel. To so great an extent does this take place in some instances, that the wall of the vessel presents the appearance of being composed of fibres. The venulæ rectæ so far pursue the same course as the arteries of the same name, that the several trunklets originating in the coalescence of a capillary circle do not immediately unite to larger trunks, but remain separate as far as to the cortical surface of the intermediate layer. But inasmuch as a small venous plexus is already present upon the papilla around the openings of the ductus papillares, that principally discharges its contents through the medulla, a few small venous trunks

pass upwards from the papilla itself. These, as they pass through the lacunar spaces or fissures, are speedily joined by others originating from the capillaries of the papillary fasciculi of urinary tubules, and these again by others proceeding from the capillaries at a somewhat higher level, and so on. From the constant accession the veins thus receive in the direction from the papilla to the cortex, their number becomes gradually increased in the cortical border of a fissure to fifteen or twenty (venulæ rectæ, fig. 150, *v r*).

As the veins surpass the arteries, not only in number, but in size, it comes to pass that the intermediate spaces dividing the fasciculi of urinary tubules from one another in the medulla are chiefly occupied by the former vessels. In the medulla itself the several veins lying contiguous to one another in any fasciculus communicate by frequent looped anastomoses. When the fasciculi have reached the cortex, the different veins they contain quickly coalesce to form several large trunks that enter the large veins of the cortex; and it usually happens that from each of the fasciculi of urinary tubules bounding a fissural space a venous trunklet arises, which receives the small veins of the adjoining parts; so that in this way each fasciculus of veins discharges itself by at least as many trunks into the nearest large vein as there are fasciculi of urinary tubuli around the fissural space.

In regard to the relation that exists between the blood-vessels and urinary tubules of the medulla, it still remains to be mentioned that the veins ascending in the axis of the fissural space do not come into contact with the collecting tubes, and are the more remote from them the nearer they approximate the surface of the cortex. They behave themselves differently, however, in regard to the limbs of the loops, the descending limb running between the venous fasciculi in the upper parts of the marginal medullary layer, when they pass from the region of tortuous canals to the fasciculi of straight medullary canals.

VESSELS OF THE FIBROUS CAPSULE.—As is usual in such fibrous membranes and fasciæ, a wide-meshed capillary plexus is distributed over the surface and in the substance of the

capsule. This receives its supply of blood partly from the small arteriæ interlobulares that do not entirely break up into the vasa efferentia of the glomeruli, and partly from the terminal branches of the surrounding arterial trunks, as of the phrenic, lumbar, and suprarenal arteries. Veins arise from the capillaries, which partly discharge themselves into the stellate veins of the cortex of the kidney, and partly into extraneous veins. The latter accompany the corresponding arteries in pairs.

LYMPHATICS.—Lymphatics of various size issue both from the hilus and from the capsule of the kidney. The former accompany the bloodvessels, but nothing is known respecting their origin. The smaller trunks of the capsule, as is rendered evident by careful injection, proceed from a plexus of small lymphatics that lie between the fasciculi of the capsule. When this plexus is injected, even under very moderate pressure, the fluid enters the parenchyma of the kidney, and penetrates into the fissural spaces dividing the tortuous canals of the cortex from each other. The small lymphatics of the capsule, as well as the larger trunks issuing at the hilus, become injected with equal facility when the fissures of the kidney are filled with fluid in consequence of obstructed flow of urine. This ready passage of the fluids of one cavity into another is facilitated by the presence of certain anatomical arrangements; but in what these consist, and whether they persistently or only temporarily favour the communication between the fissures and the lymphatics, is unknown.

CONNECTIVE TISSUE.—The *connective tissue* of the kidney does not everywhere exhibit the same structure; the fibrous capsule and the immediate investment of the large bloodvessels in the papillary portion of the medulla essentially consisting of the fibrillar form, whilst the labyrinth of the cortex and the limiting layer of the medulla chiefly consist of the cellular form of this tissue. The fibrous framework of which the capsule is composed is densest at the free surface. From its inner or attached surface numerous delicate fibres dip into the substance of the kidney between its morphological elements; these and the

bloodvessels which pass from one to the other form the loose connection between the capsule and the parenchyma of the kidney. No fibrillated connective tissue exists between the tortuous portions of the urinary tubules. An exception, however, very frequently exists, besides the above-mentioned investing layers, in the case of the tissue immediately surrounding the Malpighian corpuscles, and especially those which lie close to the medulla. These are often enclosed by fibrous connective tissue. Elsewhere only isolated small fusiform cells lie between the blood capillaries and urinary tubules of the labyrinth, which are so placed that the long axes of their nuclei stand at right angles to those of the urinary tubuli. These cells do not, however, in any way bind the convolutions of the urinary tubuli either to one another or to the bloodvessels, as can be demonstrated from the examination of kidneys affected with acute œdema and obstructed flow of urine. In such kidneys the cortex is considerably larger than that of the opposite sound organ, and the convolutions of the tubes must consequently be put considerably upon the stretch; and we may see on section a remarkable separation of the capillaries and urinary tubules. The spaces between the tubes of the medulla in the immediate neighbourhood of the papilla are filled with a distinctly fibrillated connective tissue surrounding the urinary tubuli in a concentric manner; the nearer we approximate the limiting layer, the more delicate becomes the fibrillation and the more abundant the cellular elements which give off from their fusiform or stellate bodies fine processes often of considerable length.

NERVES.—The *nerves* penetrate the kidneys with the vessels, and present ganglia in their course. Anatomical investigation has furnished us with no information in regard to their mode of termination. The results of experiment show that besides motor fibres effecting the contraction of the circular muscular coat of the smaller arteries, they also contain sensory fibres.

Historical points in reference to the anatomy of the urinary tubules in Mammalia. The straight tubuli of the medulla have been known since the time of Bellini in the seventeenth century, the tortuous since the time of Ferrein in the middle

of the eighteenth. Our knowledge of the structure of the kidneys has rapidly progressed during the last thirty years, in consequence of the application of the following methods of investigation: 1. By a comparison of the easily unravelled structure of the organ in the lower Vertebrata (Bdellostoma by J. Müller, Coluber by Bowman). 2. By more precise and definite methods of employing injections than had previously been adopted, first by the application of atmospheric pressure (Huschke); then by the use of more easily flowing material, as the solution of carmine in gum employed by Gerlach, and the mixture of glycerine and Prussian blue by Henle; and lastly, by very careful regulation of the amount and duration of the pressure applied (C. Ludwig). 3. By the discovery of means capable of effecting the solution of the connective tissue and the bloodvessels while the urinary tubules are left intact. Isaacs accomplished this by boiling fragments of kidney in very diluted acids, as in sulphuric, phosphoric, chromic, boracic, tartaric, and citric acids, and also by boiling in chloroform (?). Henle introduced the use of cold concentrated hydrochloric acid for the same purpose, and Schweigger-Seidel described the best mode of applying it. C. Ludwig found the most advantageous proceeding to consist in boiling small portions of the kidney in a mixture of hydrochloric acid and alcohol, and then to macerate them for a day in distilled water. 4. By a more accurate comparison of the structure of the tubules in different parts of the same kidney (Henle). It was thus that the discovery was made by Bowman and Gerlach that the membranous investment of the glomeruli, first described by J. Müller, was the cæcal extremity of the tubuli, and became continuous through the neck with their tortuous portion. Isaacs subsequently showed that the tortuous portion of the urinary tubuli became attenuated towards the limits of the cortex, and still more recently Henle showed that the narrowed canal formed a loop in the medullary substance; Henle also discovered at the same time that the wide canals proceeding from the papilla underwent a second division at the end of the medullary ray. The communication between the branches of the collecting tubes and the ascending limbs of the loops was then demonstrated by

C. Ludwig and Zawarykin. Lastly, the intermediate portion was first recognized to be a constantly present division of the canal by Schweigger-Seidel.

Our more accurate knowledge of the structure of the walls of the tubuli commences with Henle; he demonstrated the presence of the basement membrane of the cloudy epithelium in the tortuous, and of the transparent in the straight, tubuli; v. Wittich recognized the want of a cell membrane in the epithelial cells of the tortuous portions of the tubes; Roth discovered that the capsules were composed of endothelial cells; and Steudener, the peculiar form of the epithelial cells in the ascending limb of the loop.

The greater part of the course of the bloodvessels was easily ascertained as soon as gelatine was employed for the purposes of injection in the place of resin and wax. A few difficulties alone remain to be explained, as in particular the courses of the branches of the arteriæ interlobulares that enter directly between the glomeruli into the plexus surrounding the urinary tubules; these vessels were recognized as being commonly present in the kidneys of Mammals by Toynbee, Isaacs, and Schweigger-Seidel; the arteriolæ rectæ veræ were discovered independently of each other by R. McDonnell and Virchow.

The fibrillated connective tissue of the medulla of the kidney was first described by Goodsir; the peculiar cells of the cortex by Beer and Schweigger-Siedel.

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CHAPTER XXII.

THE ADRENALS OR SUPRARENAL CAPSULES.

By C. J. EBERTH.

In *Fishes* the adrenals lie on the anterior or posterior surface of the kidneys, in the form of small paired or multiple bodies, varying in size from that of a pin's head to that of a bean.

In the *Batrchia*, both in the anourous and urodelous genera, the adrenals form small yellowish granules, lying upon the anterior surface of the kidneys and upon the venæ renales revehentes.

In the *Saurians* the adrenals appear as yellowish bodies, situated upon the renal veins near their opening into the inferior vena cava. In the *Ophidia* they are found on the inner surface of the sexual glands, lying upon the same veins. In the *Chelonia* they occupy the same position as in Batrachia; and those of *Birds* lie at the upper border of the kidneys, immediately upon the vena cava.

Parenchyma.—The adrenals consist of two kinds of cellular masses, composing respectively the cortical and medullary substance. This terminology is sufficiently accurate for the various classes of Mammalia, since the same relations generally obtain; but it cannot be adopted for the other Vertebrata, because the two substances are not here distinctly separated into an inner and an outer portion, the cortical portion penetrating into the interior, and the medullary substance appearing at the surface.

The adrenals of the *Fish* (eel) are composed of rounded

heaps of angular and slightly stellate cells that are sometimes arranged in a single layer, and sometimes in many tiers. In the interior of these cellular masses there is usually an irregularly shaped cavity. It is still undetermined whether a medullary substance is present or absent in the adrenals of fishes.

Fig. 154.

Fig. 154. Irregularly shaped masses and columns of cortical substances from the adrenals of the Frog.

In the adrenals of *Batrachians, Saurians, Chelonians,* and *Birds,* the cortex and medulla are not arranged in layers as in Mammals, but the two substances are placed side by side, in rounded heaps, or in branched cords and columns.

In the Batrachia the most superficial portions of these organs are composed of solid roundish and elongated groups of polygonal cells, filled with fat molecules. These correspond

to the proper cortical substance. The medullary portion, which is much more sparingly developed than in other animals, is here only represented by small isolated accumulations of polygonal cells, which are superimposed on the cortical portion. In its deeper parts the latter consists of branched and anastomosing columns of cells that decussate with similar columns of the medullary substance. Both the columns and the cell-masses are destitute of a membrana propria.

The structural relations are similar to the above in *Saurians* and *Chelonians*.

The web-like arrangement of the branched cortical and medullary columns is still more distinctly marked in *Birds*. Instead of the solid columns, however, cylindrical tubes of narrow bore are found, which, like those of the cold-blooded animals, do not form a perfectly closed plexus, but frequently end cæcally. The cells of these tubes are small cylinders with excentric nucleus in the cortical portions, but more polymorphous, and usually cylindrical or polygonal, in the medullary.

In *Mammals* the two substances are arranged in a laminated manner. The external or cortical substance is greyish yellow, or, if it contain much fat, whitish yellow, in colour, and fractures in a radial direction. It invests the internal grey medullary masses in the form of a capsule, and into these also small portions of the cortex penetrate, accompanied by large vessels. No medulla exists in the thin marginal portions of the organ, but the innermost cortical layers here come into contact, and form a simple brown stria.

The accessory adrenals that are frequently found in considerable number in immediate proximity to the chief organ, in the form of yellowish granules, are detached portions of the cortex, provided with a highly vascular nucleus of connective tissue,

In Man, as a result of decomposition, the innermost cortical layers break down into a semi-fluid mass. Under such circumstances a cavity is found between the medulla and the cortex, filled with a pultaceous material composed of blood and disintegrated cortical substance.

CORTEX.—In the *Cortex*, from two to three distinct layers

may be distinguished. In the latter case there is an external and internal layer of rounded cell masses or clusters (paren-

Fig. 155.

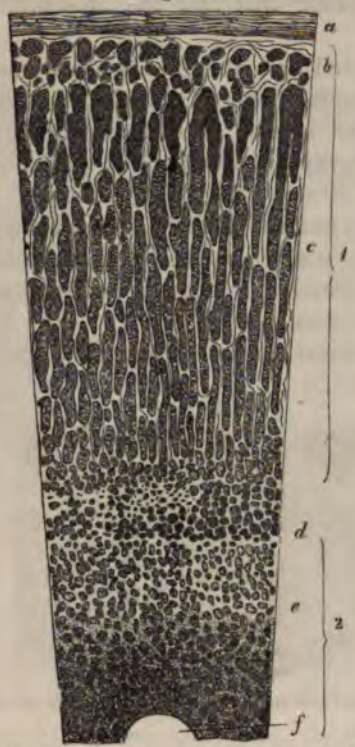

Fig. 155. Vertical section through the adrenal of Man. 1, cortex ; 2, medulla ; *a*, capsule ; *b*, layer of outer cell masses ; *c*, layer of cell columns (Zona fasciculata) ; *d*, layer of the internal cell masses ; *e*, medullary substance ; *f*, section of a vein.

chymatous bodies), separated by a layer of cylindrical columns of cells (cortical cylinders, cortical columns). This arrangement is found in Man, the Pig, Dog, Hedgehog, and Guinea-pig.

In other animals, as the Ox, Horse, Cat, Rabbit, and Mouse, the outer layer of cell masses is absent, the cortical columns coming into direct contact with the investing capsule, and being continuous below with the internal cell masses.

These several laminæ, however, are by no means so sharply

differentiated from each other as the whole cortex is from the medulla. In the first-mentioned group, and especially in Man, the outermost layer is clearly distinguishable from the second, but the limit between this and the innermost layer is very faint.

Both the external and the internal cell masses consist of polygonal and rounded balls of protoplasm containing a single nucleus, and either isolated or collected into groups. In the Ox the innermost layer appears as a tolerably homogeneous infiltration of the stroma with polygonal cells. In some other animals, as in Man and the Rabbit, the several cells appear to have coalesced into a single mass. The external cell masses of the Dog are elongated and horseshoe-shaped structures composed of columnar cells.

The cortical columns consist of elongated cylindrical masses

Fig. 156.

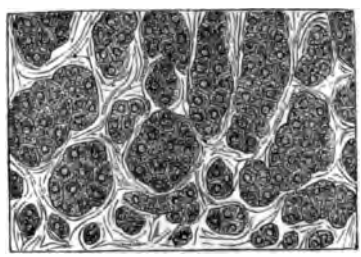

Fig. 156. Cells and cell masses of the most external cortical layer of the adrenal of Man.

of cells. As they lie in successive rows, they give to thick sections of the cortex, when examined with low powers, the appearance of being composed of long parallel bands or columns, as in Man. Just beneath the capsule many of the columns form short communications with each other. In their subsequent course, also, they sometimes appear to anastomose.

The cellular constituents are the same as in the most external layer, except that in many animals they are constantly, and in Man occasionally, infiltrated with larger and smaller fat drops.

The innermost cells of the internal cortical layer in Man are characterized by their yellowish colour.

In those animals which possess no external cell masses, the superficial columns of the cortex form shorter, frequently anastomosing, rounded, and columnar masses, or are cylinders

Fig. 157.

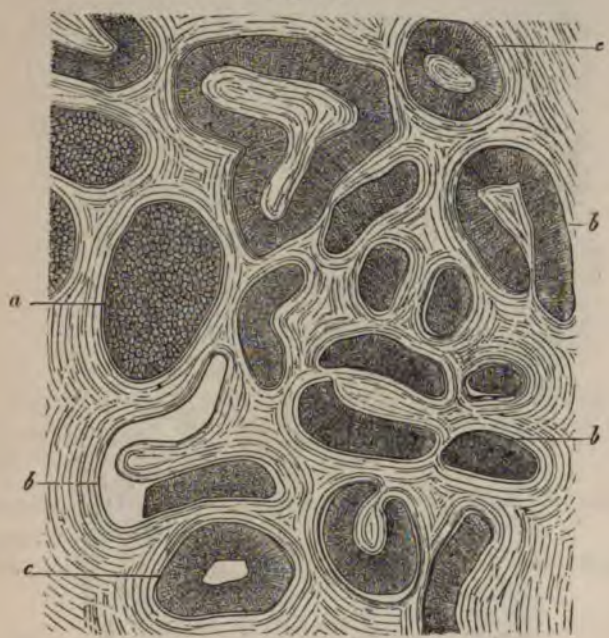

Fig. 157. Horizontal section through the most external cortical portion of the adrenal of the Horse. *a*, Closed cylinder of the surface ; *b*, channel-like and cylindrical columns of the cortex ; *c*, stroma.

that are continuous with each other by means of short arches beneath the capsule, as in the Rabbit, Mouse, and Cat. The cortical columns of the Horse are small columns, and channel-likes bodies that towards the outer parts, in consequence of the gradual coalescence of their borders, become converted into hollow cylinders with blind extremities. (Kölliker, Eberth.)

The cells of the cortical columns in the Ox are columnar or polygonal, arranged with their long diameter at right angles to the radius; in the Rabbit they are polygonal, and in the Horse they form slender cylinders. In Man, as well as in other

animals, irregular fissures or splits are not unfrequently found in the centre of both the round and cylindrical cell masses, but

Fig. 158.

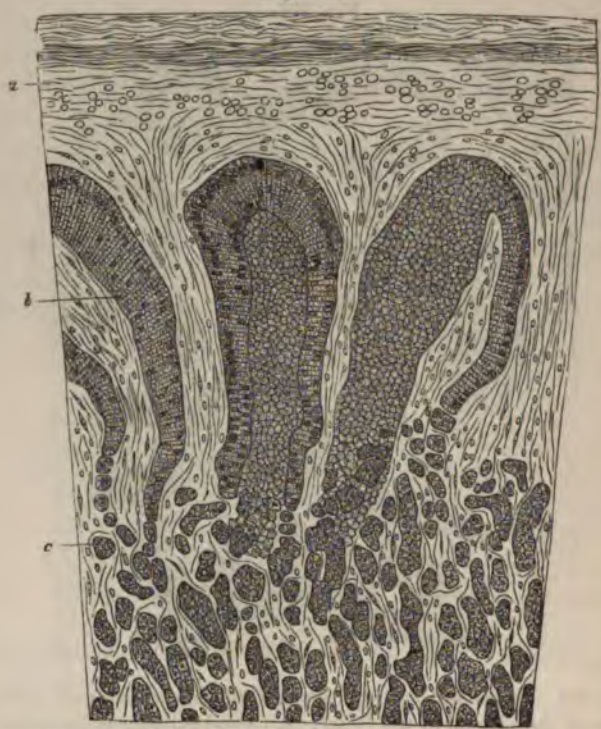

Fig. 158. Vertical section through the cortex of the adrenal of a Horse. *a*, Capsule ; *b*, cell columns ; *c*, cell masses.

I have never met with the vesicles lined with epithelium that have been described by Grandry.

MEDULLA.—Intervening between the narrow-meshed plexus of large vessels in the medulla is a spongy tissue composed of delicate connective tissue, in which lie the medullary cells. These are sometimes isolated, but are frequently also collected into rounded groups, as in Man ; or form plexiform cords, as in the Ox, Horse, Pig, Dog, Cat, Rabbit, Guinea-pig, Mouse, and

Hedgehog. Processes of these cords sometimes extend into the

Fig. 159.

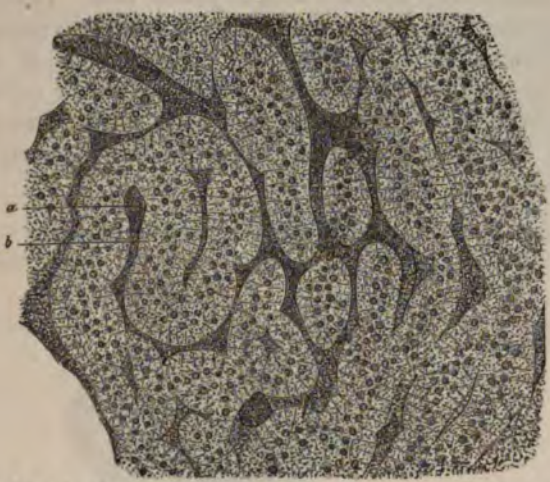

Fig. 159. Vertical section through the medullary substance of the adrenals of the Ox. *a*, Bloodvessels; *b*, cords or columns of medullary cells.

cortex, so that small masses of medullary substance may even appear upon the surface.

The cells of the medulla are very various in form, and

Fig. 160.

Fig. 160. Cell column of the medulla; from the adrenal of the Ox.

delicate in structure. In Man they are stellate and polygonal; in the Pig, frequently columnar; in the Horse and Ox, often scarcely recognizable, a finely granular mass with centric or excentric nuclei appearing in their stead, or columnar and stellate intercommunicating cells may be present in addition.

The medullary cells become stained of an intense yellow and brown colour, whilst the cortex remains unchanged, or, like other tissues, only assumes a light yellow tint. This reaction, which occurs with equal intensity in the most diverse animals, is accelerated by the action of alcohol. It is of essential service in enabling us to distinguish between the cortical and the central cells, where it is impracticable, either through their form or arrangement, to draw a precise line between the two substances.

Fig. 161.

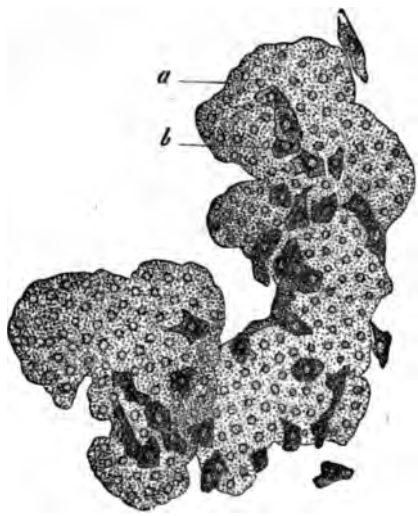

Fig. 161. From the adrenal of the Frog. *a*, Cortical cell masses; *b*, medullary cells.

In Man only a slight brown tint is produced in opposition to the intense staining that occurs in the Ox, Pig, Dog, Cat, Hedgehog, Guinea-pig, Rabbit, Mouse, and Cat; in the Pigeon, Duck, and Fowl; in the Tortoise and Lizard, and in the Frog and Salamander. I have, unfortunately, only had the opportunity of examining the adrenals of such fish as had been preserved in spirit.

THE STROMA.—From the fibrous capsule coarse processes are given off, which penetrate into the interior of the organ,

and separate off or isolate certain territories of the parenchyma (cortex). From their sides they give off fibres continuous with the lateral processes of more delicate columns of connective tissue, which again intercommunicate with each other. Between these trabeculæ are rounded or elongated spaces, filled with irregular masses and columns of cells. In the cortex the thicker connective-tissue columns quickly break up into a very delicate framework with regular polygonal meshes, each of which contains a cell.

The stroma in the medulla is still more sparing in quantity than in the cortex. It here only forms an investment to groups of cells.

I have not been able to discover any proper investing mem-

Fig. 162.

Fig. 162. *a*, Connective-tissue columns from the most external cortical layer of the adrenal of the Ox ; *b*, parenchyma cells.

branes surrounding the cell masses, such as have been described by Grandry, Henle, and others, even after maceration in acids and alkalies. It is possible that they mistook for these membranes fine membranous septa of connective tissue, or the walls of the bloodvessels, which often lie in immediate apposition to the cell masses.

BLOODVESSELS AND LYMPHATICS.—The adrenals are amongst the most vascular organs in the body. Their supply of blood is derived from the phrenic and cæliac arteries, from the aorta and from the renals. Several branches from these vessels penetrate the capsule, and accompany its processes into the central medullary portion; others form a wide-meshed capillary plexus in the capsule itself; whilst others again, after traversing this, and breaking up into fine branches, join the capillaries of the cortex.

The *veins* proceeding from the medulla discharge themselves into a large central vein, that leaves the organ by the hilus, and joins the inferior vena cava. A pair of small veins accompany each artery as it traverses the cortex, and open into the phrenic and renal veins and the inferior cava. These, according to Arnold, originate in the middle cortical layer (Zona fasciculata.)

Fig. 163.

163. Delicate framework from the innermost cortical layer of the adrenal of the Ox, with a few parenchyma cells.

The *arteries* break up in the external cortical layer into a capillary plexus, the rounded meshes of which contain the cell meshes or parenchyma corpuscles. In the second zone, by their short transverse anastomoses, these vessels form radially disposed meshes; whilst in the innermost layer they are arranged in the same manner as in the most external zone.

Arnold describes vascular knots in the most external cortical layer, but neither Kölliker nor I have been able to satisfy ourselves of their

occurrence. The diverse structure presented by the cortex renders a certain variation in the mode of division of the vessels probable.

The vessels of the medulla are derived from the capillaries of the innermost layer of the cortex. They form a narrow-meshed plexus of vessels varying in their width, often presenting considerable dilatations, and discharging their contents into the renal veins. The central portion of the medulla, according to Arnold, is fed by the arteries running in the connective-tissue trabeculæ, which communicate with the medullary capillaries.

Both the narrower cortical and the wider medullary capillaries are very thin-walled; their parietes being composed only of an endothelial tube. They lie in contact with the parenchymatous bodies, and are so firmly united with the sparingly intervening stroma as to be isolated with difficulty. This circumstance has led to the belief that there are here blood-paths destitute of walls.

LYMPHATICS.—In addition to the few superficial lymphatics described by Ecker, Kölliker, and Arnold, the last-named author describes a deep set. We may also regard the irregularly dilated thin-walled cavities observed by Moers within the gland accompanying the arteries, to be sections of lymphatic canals.

NERVES.—The adrenals are rich in nerves; the supply being derived from the ganglion semilunare, the plexus renalis, and from the phrenic and pneumo-gastric nerves. The branches enter the organ by its internal and lower border, and divide, for the most part, in the medullary substance, where they form large decussating cords, and more rarely delicate plexuses. Bi- and multi-polar ganglia are frequently observable, partly isolated, partly forming large groups in the nerves of the medulla, at their points of division (Holm and Eberth). Ganglionic cells are seldom found in the cortex. The nerves are composed of fine dark-edged fibres.

It is still doubtful whether the nerves terminate in the interior of the organ, or only traverse it in the form of an endless plexus.

It is improbable that those cells are nervous, which in the Ox are found in the region between the cortex and the medulla, and frequently form clusters accompanying the nerves; for they are smaller than the true ganglionic cells, and though somewhat larger and brighter than the cells of the cortex, they are angular, and possess no processes. They stain with carmine somewhat more quickly than the cortical cells (Holm, Eberth), and do not, like those of the medulla, become brown by the action of chromate of potash. Their arrangement most closely resembles those elements of the cortex which in thick bands accompany the larger vessels through the medulla (Holm, Eberth).

In the *Batrachia* and *Lizards* I have not been able to find any nerves in the parenchyma of the organ. They are very sparingly present in *Tortoises*. Large ganglia are found superficially situated in *Birds*, but the organ itself is rather poor in nerves and ganglion cells. Amongst *Mammals* the adrenals of the Carnivora and Rabbit are sparingly provided with nerves, whilst those of Man and of the Pig are characterized by a very large supply, though they again are surpassed in this respect by the Ox.

As the statement advanced by Luschka and Leydig, that the medulla of the adrenals consists entirely or chiefly of ganglion cells, has been shown to be incorrect, further evidence is required to prove the accuracy of the observation of Leydig, that in Selachia, the Ganoids, and Reptiles, "portions of the adrenals adhere to the several ganglia of the sympathetic, or are rather to be regarded as constituting integral portions of that nerve." These segments of the sympathetic correspond to the medullary mass, whilst in Fishes and Reptiles the cortex of the organ appears to be composed of vessels. The so-called axillary hearts in the Torpedo would represent such cortical segments. Leydig is also inclined to regard the masses of cells found in some Invertebrata, as in *Paludina* and *Pontobdella*, next the ganglia, as equivalents of the adrenals.

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CHAPTER XXIII.

THE BLADDER AND URETERS.

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THE BLADDER AND URETERS form a complex system of organs that play a passive rather than an active part, their physiological importance to all appearance being limited to receiving the urine excreted by the kidneys, and facilitating its discharge from the body. To this circumstance they owe the relative simplicity of their anatomical characters, as well as the general agreement they present in their structure.

The *bladder* possesses at its upper part a peritoneal investment that covers it to a greater extent posteriorly than anteriorly or laterally. The thickness of its walls alters with its state of distention, varying in Man, apart from local differences, between 2 and 15 millimeters.

There is a general agreement in the structure of the urinary bladder of most Mammals, and we shall therefore limit our description to the characters it presents in Man.

Amongst the Vertebrata the bladder is absent in Birds, and in some Fishes, Amphibians, and Reptiles. The urine of these animals is so rich in the salts of uric acid, that were it long retained in the bladder, a deposit of too solid a nature would be occasioned. The bladder of a few Reptiles and Amphibia (as the Tortoise and Frog) opens like the ureters into the cloaca, so that urine can be evacuated without having passed through the bladder. A similar arrangement occurs in the Monotremata amongst Mammals.

In the bladder of Man the following layers are met with proceeding from within outwards:—

I. THE EPITHELIUM.—This is arranged in many tiers, the several layers presenting the greatest differences in the characters of the cells.

Most internally are found one or two layers of cells, which, though varying much in size and form, are usually spheroidal and polyhedric, or, especially when large, are somewhat flattened. Their borders and angles are often so prolonged that their under surface presents a concavity into which a cell belonging

Fig. 164.

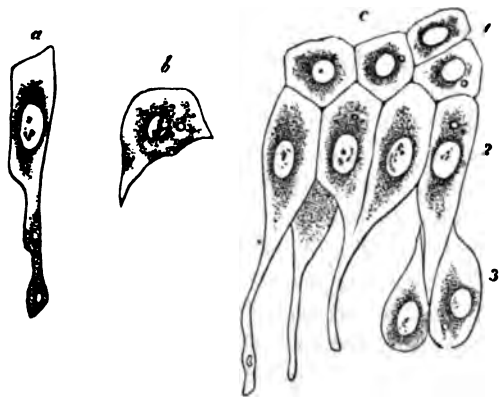

Fig. 164. Epithelium of the bladder. *a*, One of the cells of the second row; *b*, a cell of the first row; *c*, exhibits the first, second, and third layers of the epithelium *in situ*.

to the next series is received. The contents are moderately granular, with one or two nuclei and distinct nucleoli. These correspond to the cells that are frequently found in urine that has been passed. In some instances delicate perfectly hyaline bodies may be seen, which throw out projections at one or several points of their walls without the occurrence of any shrivelling or other change, an appearance that is exhibited also by other epithelial cells.

The next layer of epithelial cells (fig. 164, *a*, *c* 2) is distinguished from the rest by the regularity of the arrangement of

its elements; corresponding nearly to each other in size (being about 0·03 of a millimeter in their longest diameter) the cells present a conical form, with their broad convex bases directed towards the surface. The apices directed towards the deeper tissues are prolonged into an unbranched and often varicose process of various length, reminding the observer of the epithelial cells of the nasal mucous membrane.

It is not easy to ascertain the further course of those peduncles or processes which penetrate into the deepest layers of the epithelial cells, yet it appears highly probable that they establish a connection between the cells and the most superficial layers of the connective tissue immediately subjacent to the vesical epithelium, joining either with the connective tissue or with the nervous elements. In favour of this view is the fact that, however carefully the cells may be isolated, the processes never end in a point, but always give the impression of not having been obtained in their integrity; or, in other words, of having been abruptly broken off. An additional argument is derived from the fact, that, after the epithelium has been detached, fine fibres, curled at their extremities, and of equal size with the processes of the cells, project from the surface of the connective tissue, and occasionally it may even happen that appearances are presented indicating an immediate connection between the two structures.

The frequently discussed question of the origin of epithelial cells from subjacent connective tissue may obtain some elucidation from these relations.

The deepest or most external layer of the epithelium (fig. 164, *c* 3) is composed of rather irregular oval cells, which are frequently elongated towards the surface, their extremities being intercalated between the conical ends of the cells of the above-mentioned layer.

II. THE CONNECTIVE-TISSUE LAYERS.—A layer of very dense, finely fibrous connective tissue, containing numerous nuclei, and of about 0·02 of a millimeter in thickness, lies immediately beneath the epithelium, and is sharply differentiated from an external layer that contains fewer connective-tissue corpuscles and thicker bundles of fibrillæ, and varies from 0·8 to 1·5

millimeters in thickness. This last is traversed in various directions by numerous elastic fibres, and a not inconsiderable number of smooth muscular fibres, which are partly isolated and partly associated into fasciculi.

Near the urethral orifice, solitary acinous glands are found scattered here and there, similar to those met with in the pars prostatica urethræ. They are by no means constant, and appear to be especially infrequent during the earlier periods of life, which is perhaps referable to their development taking place long subsequent to birth. The relations of the vessels and nerves will be discussed hereafter.

III. THE MUSCULAR LAYERS.—The fibres of the muscular coat of the bladder are from 0·1 to 0·25 of a millimeter in length, and possess a distinct elongated, rod-like nucleus. In the urinary bladder of the Frog the muscular fibres are of remarkable length, amounting to as much as 0·4 of a millimeter or more.

The fibres of the bladder in Man unite to form rounded fasciculi and cords, having a diameter of 0·03 to 0·15 of a millimeter, and being separated by septa of connective tissue, in which run bloodvessels and nerves. These sheaths vary in size, both locally and individually, but in general are much thicker in children than in adults, and in the former may equal or even exceed the muscles themselves. In the vicinity of the sphincter vesicæ the muscular fasciculi are completely separated from one another, and enclosed by the interstitial connective tissue, which so interpenetrates the fibres as either to isolate them entirely, or to allow only a few to be combined together.

The course of these muscular fibres is by no means regular, and differs in many particulars from any schematic representation.

If, however, such a representation be desired, the simplest, and that most in accordance with facts, would be the following. Most internally is a plexus of circular muscular fasciculi, decussating at acute angles, and forming transverse meshes. These fibres are particularly strongly developed at the ostium internum urethræ; here the course of the fasciculi is more

definite, running parallel to each other, and forming a complete ring at the orifice of the bladder, the sphincter vesicæ. Externally to this circular layer follows the layer composed of longitudinal fasciculi, which gradually predominates towards the vertex, and in children may be observed to be continued into the partially or completely obliterated urachus. It is impossible to give more minute details respecting the course of the muscles, since, in the various bladders I have examined, the variations have been so great that a minute description is only applicable to the individual specimen.

The *Trigonum lieutodii* consists merely of a thickening of the connective tissue with all its elements, extending from the orifices of the ureters to the Caput gallinaginis.

The *vessels* of the bladder, the Arteria vesicalis superior and inferior, proceeding from the posterior wall of the Arteria hypogastrica, are chiefly distributed to the fundus. They penetrate the muscular layer of this part obliquely, giving off a few small branches to it as they traverse it, and are distributed in the connective-tissue layer about midway between the epithelium and the muscular tissue, and nearly parallel to the surface. From these trunks small branches ascend vertically towards the epithelium, immediately beneath which, separated only by a layer of fibrous tissue that is sometimes scarcely perceptible, they form a close and delicate capillary plexus. If the bladder be thrown into folds, these small branches occupy the middle of the fold, and are thus preserved from angular bends and curves.

The *nerves* may be followed as medullated fibres in the connective-tissue layers, especially at the fundus near the urethral orifice, where they are present in great numbers. It is difficult to form a correct judgment on their mode of termination. Kisselew considers that they end in peculiar cells of the epithelial layer, distinguished from the rest by their becoming more strongly tinted with carmine, and by their firmer adhesion to the subjacent connective tissue. He seems, however, only to have had objects similar to the migrating cells under observation. A few ganglion cells are found, though only very sparingly, in the course of the nerves.

Medullated nerve fibres can be beautifully followed in the

bladder of the Frog. Their convolutions surround large yellow ganglion cells, provided with a thick epithelial layer, first described by Jacubowitsch.

URETERS.—The ureters exhibit, as was stated at the outset, a very similar structure to that of the urinary bladder. The epithelium exactly resembles that of the bladder, and beneath it is a layer of connective tissue, followed by a threefold muscular tunic; of which the innermost layer is longitudinal, the middle circular, and the external, which is the thinnest, possesses a less regular but essentially longitudinal course. A thin layer of connective tissue forms a tunica adventitia, and is the most external of the layers investing the ureters.

The bloodvessels behave like those of the bladder. Engelmann * describes them as forming a subepithelial plexus in the Rabbit, on which the epithelium is directly seated, without the intervention of any connective tissue. In Man, however, the layer of capillary vessels is less superficial and consequently more protected.

A small number of medullated nerves penetrate the ureter. I have not been able to demonstrate the presence of ganglion cells, except in the plexus of the adventitia, termed "fundamental" by Engelmann.

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* Pflüger's *Archiv für Physiologie*, 1869, Band ii., Heft 4 and 5.

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CHAPTER XXIV.

THE TESTES.

By v. LA VALETTE ST. GEORGE.

External Portions of the Testes.

The male sexual organs are tightly packed in a dense fibrous membrane, the *tunica albuginea*, which is continued upon the upper part of the excretory duct or epididymis.

The external surface of this fibrous membrane is smooth and polished, in consequence of the covering it receives from the *internal or visceral layer* of the *Tunica vaginalis propria*. Where it covers the testis, this is indissolubly connected with the albuginea, as the *tunica adnata*, but it is less firmly

Fig. 165.

Fig. 165. Villi of the serous membrane with columnar epithelium. *a*, Vascular loops ; *b*, epithelium ; *c*, nuclei.

adherent to the epididymis. The tissue of the serous membrane is often prolonged into villous-like excrescences, which have been described in detail by v. Luschka,* and are found both at the sharp border of the epididymis and upon the upper

* Virchow's *Archiv*, Band vi., p. 321.

border of the testis itself. These processes are covered by one or several layers of tesselated epithelium, or by scattered spheroidal cells. Cells have also been observed presenting an irregular form, and constrictions.

I have frequently seen such "villi of the serous membrane" seven millimeters in length, and four millimeters in breadth, invested by columnar cells.

Elsewhere the epithelium of the Tunica adnata, as it can easily be obtained by shaving off sections, consists of a layer 8 μ in thickness, of variously sized polyhedric cells, with sharply defined oval nuclei, and one or two nucleoli. The contents of the cells are finely granular, and sometimes exhibit small fat-drops. To the head of the epididymis, and to the

Fig. 166.

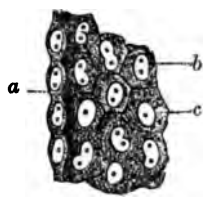

Fig. 166. Epithelium of the Tunica albuginea. *a*, Folded border; *b*, cells; *c*, nuclei.

upper part of the testes, are attached the so-called Hydatids of Morgagni; of these the superior, which is either solid or hollow, with a more or less elongated pedicel, may be regarded as the remains of Müller's duct; whilst the inferior, of a flattened clavate form, sometimes, according to v. Luschka,* communicates with the canal of the epididymis.

The body described by Giraldès,† Henle,‡ and Kölliker,§ under the names of *Corpus innominatum*, *Parepididymis*, and *Organ of Giraldès*, consisting of a convoluted mass of

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* Virchow's *Archiv*, Band vi., p. 310.

† *Bulletin de la Societé Anatom. de Paris*, 1857, p. 789. *Journal de la Physik*, Band iv., p. 1.

‡ *Handbuch der Eingeweidelehre*, p. 364.

§ *Handbuch der Gewebelehre*, p. 537.

closed tubules the two extremities of which are dilated, and which lies between the head of the epididymis and the vas deferens, is perhaps analogous to the Parovarium, and to be regarded as the remains of the Wolffian body.

The *Tunica albuginea*, or fibrous investment of the testis, is formed of connective tissue with a sparing quantity of delicate elastic fibres; its thickness increases towards the posterior border, where it penetrates into the interior of the gland as the mediastinum testis, or corpus Highmori. In addition to this, it sends off from every part of its internal surface, besides isolated fasciculi of connective tissue, flat processes, *the septula testis*, which run towards the mediastinum.

The *parietal lamina* of the tunica vaginalis propria, like the visceral, is composed of connective tissue traversed by fine elastic fibres, and is lined on its internal surface with a similar flattened epithelium.

The tunica vaginalis propria is enclosed in a second investment of connective tissue, the *tunica vaginalis communis*, which becomes denser towards the apex of the testis, but in the upper parts exhibits a loose laminated structure.

Upon the inner surface of this, between it and the propria, and united to both membranes, Kölliker discovered smooth muscular fibres, which have since been described by Henle as a *cremaster internus*, and, according to Rouget,* may be traced upon the septula testis. On its surface the fan-like expansion of the cremaster externus is spread, the fasciculi of which are surrounded by elastic plexuses. According to Rektorzik,† it also supports small non-vascular, rounded, and in part pedicellate excrescences. The outermost investment of the testis is formed by the scrotum, the subcutaneous cellular tissue of which contains both isolated and plexiform fasciculi of smooth muscles, which, according to Treitz,‡ arise by elastic tendons from the anterior surface of the os pubis, the ligamentum suspensorium penis, and the crural fascia. This *tunica dartos*, first accurately described by Kölliker, adheres by

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* *Comptes Rendus*, Tom. iv., p. 902.

† *Wiener Sitzungsberichte*, 1837, p. 154.

‡ *Prager Vierteljahrsschrift*, 1853, Band i., p. 113.

means of loose connective tissue, that exhibits posteriorly a layer of fat,* to the tunica vaginalis communis, and forms in the median line the septum scroti, that divides the scrotum into two halves. It is covered by the skin, which contains large sebaceous and sudoriparous glands, and supports a strongly pigmented epidermis.

Internal Anatomy of the Testis.

Structure of the Tubuli Seminiferi.—The septula testis divide the organ into a series of compartments within which the proper gland substance is contained,—the *lobuli testis*.

These consist chiefly of the *tubuli seminiferi*, or *canaliculi seminales*, that are much convoluted, and which, anastomosing with each other towards the surface of the organ, run towards the mediastinum. Near this they pursue a straighter course, and, uniting with each other, penetrate the corpus Highmori, where by their intercommunication they form the *rete testis*. From the upper part of this from twelve to fourteen canals proceed, that by increasing convolution assume a conical form, and as the *coni vasculosi* form the head of the epididymis, one after another discharging themselves into the canal of the epididymis.

This very tortuous tube lies like a clasp at the posterior border of the testis, gives off the cæcal vas aberrans, and as it recedes from the testis becomes continuous with the ascending *vas deferens*, which is at first looped, but subsequently runs in a straight direction.

As regards the commencement of the tubuli seminiferi, the greater number of authors (J. Müller, Krause, Berres, Beale, Sappey, Kölliker, v. Luschka) agree in stating that they begin partly by simple closed extremities, and partly by anastomoses. I have myself frequently found rounded and closed processes in the tubuli seminiferi of the child after maceration in acetic acid.

The average diameter of the tubuli seminiferi is 0·2 of a millimeter, the thickness of their wall varies with the degree of distension present.

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* Henle, *Handbuch der Eingeweidelehre*, p. 420.

There are still some differences of opinion with regard to the nature of the membranous walls. According to the older statements of Henle,* which, as he himself in a later published work† supposes, were founded on examinations of the smaller Mammalia, it is hyaline and structureless, with a few elongated oval nuclei. Lereboullet,‡ describing them in the Rabbit, likewise terms them structureless. Valentin § considers that a middle muscular layer can be demonstrated, lined internally by a layer of pavement epithelium, and covered externally by a perfectly clear and transparent membrane, containing elongated cell nuclei. Gerlach || finds that differences occur in the structure of the tubules in newly born and young animals, on the one hand, and adults on the other. In the former the

Fig. 167.

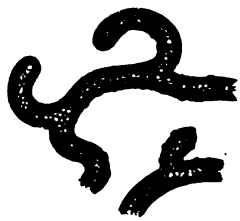

Fig. 167. Tubuli seminiferi of a year-old Child with cæcal extremities.

walls consist of a perfectly transparent structureless membrane, with a variable number of elongated cell nuclei; in the latter there is an external fibrous layer of connective tissue, with scattered elongated oval nuclei. Henle¶ gives the following description of the membrane of the tubuli seminiferi: "In longitudinal sections of the tubules it appears longitudinally, in transverse, concentrically striated; in both aspects, dark rod-shaped nuclei appear between the striæ; when spread out and examined from the surface, it is homogeneous, with

* *Allgemeine Anatomie*, p. 926.
† *Handbuch der Eingeweidelehre*, p. 354.
‡ *N. A. Acad. Nat. Cur.*, Vol. xxiii., p. 10.
§ *Handwörterbuch der Physiologie*, v. R. Wagner, Band i., p. 785.
|| *Handbuch der Gewebelehre*, p. 367.
¶ *Handbuch der Eingeweidelehre*, p. 353.

tolerably regularly arranged and very pale circular nuclei. We may therefore consider it to possess a lamellar structure, and to be composed of flat scales with flattened nuclei."

Frey* distinguishes two layers, a structureless membrana propria, and an external dense tunic of a fibrous and striated nature, with elongated nuclei, and appends illustrations taken from the testes of the Calf and of Man.

According to v. Hessling,† the tubuli seminiferi are composed of a structureless glandular membrane, or membrana propria, with a thickness of 1 μ; and externally, of a finely striated lamellated tunic of connective tissue with elongated roundish nuclei, which is 3 μ in thickness, and is sharply differentiated from the remaining interstitial connective tissue.

Kölliker‡ terms the investment of the tubules a fibrous membrane, on the inner surface of which a membrana propria can easily be demonstrated by the action of caustic potash.

Letzerich§ admits for the Rabbit only a structureless membrane, with pale elliptical nuclei.

I myself found in a one-year-old child, after maceration of

Fig. 168.

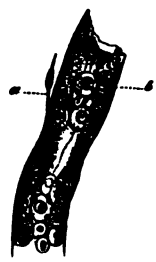

Fig 168. Portion of a seminiferous tubule from the embryo of a Cow. *a*, Adventitia ; *b*, propria.

the testis in acetic acid, that the contents of the tubules were surrounded by a very fine structureless membrane, external to which was a thick adventitia, with numerous nuclei.

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* *Handbuch der Histologie*, p. 607.

† *Grundzüge der Gewebelehre*, p. 328.

‡ *Handbuch der Gewebelehre*, p. 521.

§ Virchow's *Archiv*, Band xlii., p. 570.

The tubuli seminiferi of the embryo of a Cow, eight inches in length, as well as those of a Calf, examined in the fresh state, exhibit a tolerably thick structureless membrana propria, and a tolerably thick nucleated adventitia.

In the Dog, Guinea-pig, and Rabbit I have also been able to distinguish two tunics.

On the other hand, in the tubuli seminiferi of the adult Man I can only discover the single membrane which has been so completely and accurately described by Henle.

Peculiar cell masses, first noticed by Kölliker,* are found imbedded in the interstitial connective tissue between the tubuli seminiferi, and are to be accounted as indifferent cells of the connective tissue.†

Leydig‡ also holds the same opinion, maintaining it to be a fact of general application for the testes of all Mammals, that the connective tissue uniting together the seminiferous tubules contains also a cellular mass, which, though only present in

Fig. 169.

Fig. 169. Portion of a seminiferous tubule from the Calf. *a*, Adventitia; *b*, propria.

small quantity, follows the course of the bloodvessels, and everywhere surrounds the seminiferous tubules, where it is developed to a considerable extent. In the Boar it undergoes so remarkable a development that a section of the testis presents a chocolate colour; and the same occurs in the Horse. A similar material is also found in the Lizard.

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* *Mikroskop. Anatomie*, Band ii., p. 392.

† *Handbuch der Gewebelehre*, p. 524.

‡ *Lehrbuch der Histologie*, p. 594.

Henle* has very carefully examined these interstitial columns of cells, and has sketched the appearances presented. He states that they consist of a finely granular substance, not unlike the contents of the ganglion cells, that includes nuclei which from their uniform and small (3 μ) size, spheroidal form, and the generally apparent central nucleolus, can be readily distinguished from the variable nuclei of the cells lining the tubuli uriniferi. Henle regards it as an essential constituent of the gland, though unable to assign to it any functional value. From this recapitulation of the different views that have been held, it is easy to see that the determination of the nature and function of these cell heaps remains enigmatical.

After the seminiferous tubules have entered the mediastinum testis, they lose their proper wall, and become continuous with the more or less dilated and irregular canals of the *rete testis*.

The *vasa efferentia* are thicker than the afferent tubes, being from 0·6 to 0·4 of a millimeter in diameter, and possess a special layer of smooth muscular fibres in their investment.

CELL CONTENTS OF THE SEMINIFEROUS TUBULES.—The contents of the tubules consist of cells, the external layer of

Fig. 170.

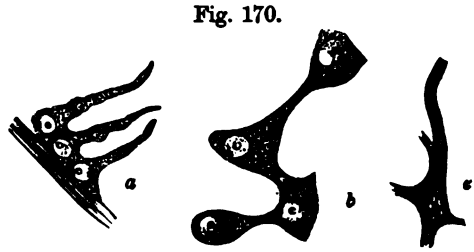

Fig. 170. Cells of the outer layer of the tubuli seminiferi. *a*, *b*, from the Bull; *c*, from the Dog.

which has been termed their epithelium. Though I cannot admit the correctness of this nomenclature, I am nevertheless able to demonstrate that the cells constituting this peripheral

* *Handbuch der Eingeweidelehre*, p. 358.

zone possess a peculiar form. According to Kölliker,* Sertoli describes these cells, after treatment of the testis with a solution of corrosive sublimate containing 0·5 per cent., and subsequent maceration in water, as branched and intercommunicating, a statement which Kölliker considers to be correct, as he has met with similar appearances in preparations obtained by maceration in caustic potash. Unfortunately the work of Sertoli is not accessible to me, but I feel sure that the cells are exactly the same as those which I here depict from the Steer and Dog, after treatment of the testis with chromic acid (¼ per cent.), or with a solution of iodine in serum for twenty-four hours.

Merkel† also discovered these cells, and considered that they form a sponge-like cellular plexus everywhere lining the interior of the tubuli, without any fibres, but with only flat anastomosing processes. The significance of these cells is still unknown. The contents of the seminiferous tubules, as Henle has correctly stated, frequently exhibit a radial disposition. To the above-described cells of the peripheral zone succeed several rows of other cells, differing both from these and *inter se*, yet still hav-

Fig. 171.

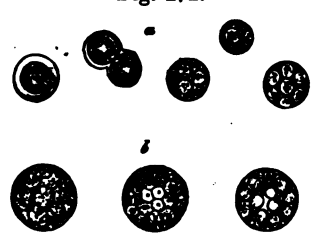

Fig. 171. Seminal cells of the Dog and Bull. *a*, uni- and multi-nucleated cells from the seminiferous tubules of the Dog; *b*, multi-nucleated cells from the Bull.

ing the same functional significance, and may hence be shortly called seminal cells. Two principal types may be distinguished, one with dark granular nuclei, and another containing clear nuclei, either with or without nucleoli. The number of the

* *Handbuch der Gewebelehre*, p. 530.

† *Göttinger Nachrichten*, 1863, No. 1, p. 7.

nuclei varies considerably; cells with one and two nuclei are most common, though as many as three or more may be present.

Many of the forms furnish indications of the occurrence of energetic processes of cell multiplication. Thus we meet with

Fig. 172.

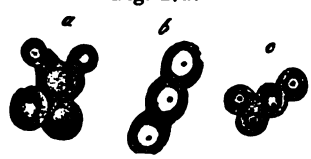

Fig. 172. Budding cells and cell chains. *a*, from the Chaffinch; *b*, from the Goldfinch; and *c*, from the common Frog.

budding cells, and chains of cells, very similar to the egg chains of Pflüger.*

Amongst the Vertebrata, multiplication by budding or germination is very common; in this mode originate the

Fig. 173.

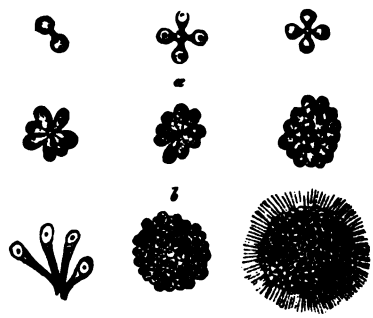

Fig. 173. *a*, Seminal cells from the Fischegel (Horse Leech?) in process of multiplication; *b*, ditto from the medicinal Leech.

mulberry-shaped masses found in the testes of many of the lower animals. Annular constriction of the nucleus, similar to that which precedes division, may frequently be observed, especially in young animals.

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* *Ueber die Eierstöcke der Säugethiere und des Menschen*, p. 53.

Both the uni- and the multi-nucleated seminal cells, besides these indications of multiplication, exhibit yet another evidence of the possession of life in the amœboid movements that I first discovered in them,* and have since ascertained to be present in almost all animals.

In the common Frog, and the edible garden Snail (Helix pomatia), I have even observed non-nucleated masses, probably undeveloped remains of protoplasm, undergoing very lively changes of form; and similar observations have been made by Grohe† and by Stricker,‡ in another domain of investigation, namely, in the milk during the puerperal state. The vasa efferentia are lined by a simple columnar epithelium with short cilia, whilst in the canal of the epididymis the cells are much elongated,

Fig. 174.

Fig. 174. *a*, Cell, and *b*, nucleus from the testis of the common Frog.

have oval nuclei, and a brush of long cilia. Beneath these is a second layer of small round cells with circular nuclei. O.

Fig. 175.

Fig. 175. Amœboid corpuscles from the testes of the common Frog (Rana temporaria).

Becker also found ciliated cells in the Hydatids of Morgagni, and I am able to corroborate his statement.

VARIOUS FORMS OF THE SEMINAL ANIMALCULES.—Besides the above-mentioned cellular elements, which line or fill the interior of the tubuli seminiferi, we meet, in sexually mature

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* *Ueber eine neue Art amöboider Zellen* ("On a new kind of Amœboid Cell"). Schultze's *Archiv*, Band i., p. 68.

† Virchow's *Archiv*, Band xxxii. p. 416.

‡ *Wiener Sitzungsberichte*, 1866, p. 184.

animals, and usually in the centre of the seed-preparing portions of the gland, with structures of characteristic shape —the seminal animalcules—which were discovered in the discharged semen of man by Johann Ham, of Arnhem,* and since then frequently described under the different names of Spermatozoa, Spermatozoids, Spermatoidia, and Zoosperms.

These constitute the male element of the generative process; they are constant only in each species, but otherwise present great variety of form in the animal kingdom.

PROTOZOA.—Spermatozoa have been already shown to be present in all forms of animal life. They even exist amongst the Infusoria. In these they were first described by Johann Müller as thread-like bodies in the *Paramecium aurelia*, occupying the interior of the enlarged nucleus, and have subsequently been further examined by Claparède, Lachmann, Lieberkühn, Balbiani, and Stein.

In the *Sponges* (*Spongilla*) Lieberkühn discovered zoosperm-like corpuscles consisting of an oval head and a thread-like body.

CŒLENTERATA.—The spermatoza of the cœlenterata possess a round or elongated head, with thread-like body—*Actinia Hydra, Chrysaora, Eudoxia, Rhizostoma, Athorybia* (v. Siebold, Kölliker, Heine, Busch, Gegenbaur).

ECHINODERMATA.—A very similar form is found amongst the Echinodermata, viz., a spheroidal body, with a fine hair-like tail—*Holothuria, Spatangus, Echinus, Asteracanthion* (Valentin, Peters, Kölliker).

VERMES.—This class presents great variety in the form of the spermatozoa; whilst the *Cestodes* and *Trematodes* (v. Siebold, Kölliker), with the *Turbellaria* (Max Schultze) possess capilliform spermatozoa, we meet in the *Nematode* worms with very peculiar structures, the shape of a rod or club (Reichert, Schneider, Meissner, Claparède). Schneider observed amœboid movements in them. According to Max Müller,

* Halbertsma, *Archiv für die Holland. Beiträge*, 1866, p. 232.

Sternaspis possesses short spermatozoa that are pointed at one end. In the *Earthworm* the spermatozoa are somewhat thickened at one end, and in *Branchiobdella* they are very much attenuated, and spirally coiled at one extremity (v. Siebold).

In the ANNELIDA spermatozoa are found with spheroidal or pyriform heads and attenuated body: *Phyllodoce, Syllis,* (Ehlers, Keferstein).

ARTHROPODA.—The seminal animalcules of the Arthropoda are of especial interest in consequence of their diversity of structure. Thus Leydig describes the spermatozoa of Notomata Sieboldii to be sickle-shaped bodies with nucleus and nucleolus, and an undulating membrane at one border. He likewise observed thick rod-like bodies with a central thickening. *Two* forms of spermatozoa are consequently here present in the same individual.

The CIRRIPEDIA, as *Balanus* and *Lepas,* possess also simple capilliform spermatozoa (v. Siebold, Kölliker). Frey and Leuckart describe the spermatozoa of *Caligus* as egg-shaped bodies having the genetic significance of nuclei. In *Cyclops quadricornis,* according to Zenker, they are rod-shaped with two coils; in Cyclopsine, according to v. Siebold, they are of oval form.

The spermatozoa of OSTRACODA, according to the statements of Zenker and Metschnikow, possess a very remarkable and highly complex form. In *Cypris ovum* they are three times the length of the entire animal, and have the form of a coiled rod, bordered lengthwise by a spiral plate. A similar anomalous form is exhibited by the spermatozoa of *Cythere viridis.* According to Zenker, these are provided with a lash having one broad abrupt extremity, and a more pointed one to which a pedicle is attached at right angles, that appears to be twisted like a ribbon round its axis. *Argulus,* according to the observations of Leydig, possesses spermatozoa, whilst the seminal corpuscles of the PHYLLOPODA (*Artemia, Branchipus*) he examined were cellular in form. They appear to be vesicular structures, with a diameter of 3μ, and marked with clear spots. The seminal corpuscles of the *Daphnidæ* are described by Leydig as being usually small rod-like corpuscles; in a few

instances he observed cells with nuclear structures, and with long and stiff rays—*Daphnia rectirostris*. The genus Polyphemus possesses uncommonly large stellate cells.

In the seminal corpuscles of these animals, as well as of other Daphniæ, Leydig observed transient amœboid movements.

DECAPODA.—We have been made acquainted with the very peculiar seminal corpuscles of the Decapoda by the observations of Henle, v. Siebold, Kölliker, Frey, and Leuckart. They are small cell-like, thick bodies, that give off fibrous processes like rays. Owsjannikow made the important observation that these rays can be withdrawn, so that the corpuscle can assume a spheroidal form.

Mysis possesses capilliform spermatic elements (v. Siebold, Frey, and Leuckart).

The spermatozoa of *Crangon* and *Palæmon*, according to v. Siebold's investigations, form flattened vesicles, from the centre of which a short spur projects.

AMPHIPODA AND ISOPODA.—Those of Amphipoda and Isopoda are stiff threads that are either pointed at both extremities (*Oniscus*), or have at one end a cylindrical pointed appendage (*Asellus*). In these woodlice the upper part of the thread is angularly bent, and easily breaks near the head; a circumstance which has caused Zenker to ascribe two forms of spermatozoa to these animals.

ARACHNIDA.—In the different groups of this class great diversity exists in regard to the form of the seminal elements. According to Kölliker, *Scorpio Europæus* possesses spermatozoa of simple hair-like form that move with activity; those of the *Tardigrada* are fusiform with an oval head, from whence proceeds two vibrating terminal threads (Doyère, Greeff).

Amongst the *Araneidæ* we find motionless round or reniform bodies, with round or elongated nuclei: *Tegenaria*, *Lycosa* (v. Siebold).

The *Acaridæ* have spheroidal, fusiform, club-shaped, and rod-like spermatozoa—*Trombidium*, *Bdella*, *Hydrachna*, *Ixodes* (v. Siebold). In the contents of the testis of *Alax*,

Claparède observed cellæform spermatozoa, *i.e.*, spheroidal corpuscles, with small rod-like nuclei.

MYRIAPODA.—The spermatic elements of the Myriapods present two distinct types. Those of the Chilognatha are fusiform, conical or cocked-hat-shaped rigid bodies, as in *Glomeris* and *Iulus* (Leuckart), whilst those of the Chilopoda possess long threads which exhibit movements (*Lithobius*, *Geophilus*, Stein).

INSECTA.—The spermatozoa of Insects are invariably capilliform threads pointed at both extremities. Their movement is sinuous or wavy, one end is often rigid, and in diluted fluid the zooid often revolve, forming a series of circles. One form alone differing from this simple one has been described by v. Siebold, in Locusta and Decticus. These grasshoppers possess an angular appendage adherent to one end of the elongated body of the zooid.

Fig. 176.

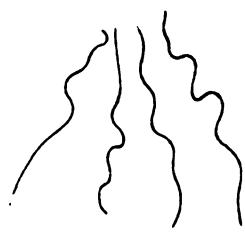

Fig. 176. Spermatozoa of Blaps mortisago.

MOLLUSCA.—The seminal elements of BRYOZOA have usually the form of a pin, with a more or less flattened head: *Alcyonella* (v. Beneden, Dumortier). In *Flustra carnosa* they are linear, and slightly sinuous; in *Alcyonidium gelatinosum* they exhibit a pointed body, with a flat and a bulging side, and with an attached fibre which is thickest in the middle (Kölliker).

In the SALPIDÆ the hair-like form reappears, whilst in the ASCIDIA the head is cylindrical, pyriform, or elliptical, and the body capilliform (Kölliker). In the LAMELLIBRANCHIATA, cylin-

drical, oval, or pyriform bodies occur with delicate capilliform tails—*Cyclas, Unio, Anodonta*, etc. (Wagner, v. Siebold).

The seminal corpuscles of the CEPHALOPHORA present great diversity of form. Gegenbaur describes those of the PTEROPODA as thickened at one end, and there slightly twisted, whilst the other end is continued into a fine thread which, just before its termination, dilates into a small vesicle.

Fig. 177.

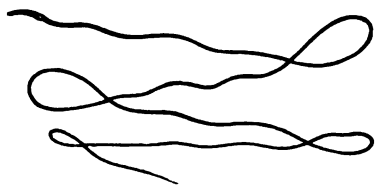

Fig. 177. Spermatozoon of Helix nemoralis.

In the GASTEROPODA the seminal elements present very various forms; in some the head is oval, pyriform, or sometimes constricted in the middle—*Chiton, Trochus, Patella, Haliotis* (Kölliker, Wagner, Erdl); in others the zooid is capilliform and pointed at both extremities—*Turbo, Buccinum, Purpura.* In *Doris* the fibre increases in thickness towards the extremity,

Fig. 178.

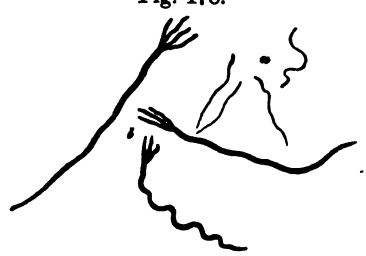

Fig. 178. The two forms of spermatozoa in Paludina vivipara.

and appears slightly twisted; occasionally there is a pointed head at one extremity—*Lymnæus, Planorbis, Helix* (v. Siebold, v. la Valette St. George).

The occurrence of *two* forms of spermatozoa, as described by v. Siebold, and subsequently by Leydig in *Paludina vivipara,*

is highly remarkable. One form is short, and twisted like a corkscrew at its upper end, whilst the other is larger, and presents a rod-like form. From the thicker end of the latter springs a brush of short fibres.

The spermatozoa of the HETEROPODA consist of elongated and anteriorly rather thickened bodies, while posteriorly they run out into fibres that gradually become more and more attenuated—*Atlanta carinaria* (Milne-Edwards, Gegenbaur).

In the CEPHALOPODA the zooids are cylindrical, with a delicate capilliform appendage—*Loligo, Sepia, Sepiola* (v. Siebold, Milne-Edwards, Peters); or they form hair-like structures—*Octopus* (Philippi).

PISCES.—The spermatozoa of *Amphioxus*, according to Kölliker, are thread-like bodies with roundish heads, and those of the *Petromyzidæ* are rod or egg-shaped, as in *Petromyzon fluviatilis*, and *marinus* (Ecker, J. Müller). The spermatozoa of the Osseous Fishes in general have very small pin-shaped bodies —*Perca, Cyprinus* (Wagner, Kölliker). In *Cobitis* there is a second enlargement below the head (Wagner, Ecker). Those of the *Salmonidæ* have an elongated head, pointed anteriorly so as to resemble the heart on playing-cards, and consisting of two parts, separated from one another by a slight groove (Owsjannikow).

The seminal corpuscles of *Sharks* and *Rays* are far larger, and are provided with a fusiform and frequently spirally twisted head—*Squalus, Torpedo, Raia* (Wagner, Ecker, v. la Valette St. George).

AMPHIBIA.—The spermatozoa of the *Tritons* and *Salamander* are very remarkable objects, and have been the subject of careful investigation (v. Siebold, Czermak). The fusiform head is continuous with a long thread, to the margin of which an undulating border is attached like a frill.

In *Pelobates* the head is very long and spirally twisted (Wagner, Leuckart).

The seminal elements of *Bombinator* are fusiform in shape. As in the Salamander, a delicate undulating membrane is attached to the sides of their bodies (Wagner, Leuckart, v. Siebold).

The *Frogs* of this country, *Rana esculenta* and *temporaria*, present this difference in the form of their spermatozoa, that in the former the capitate extremity is thick and cylindrical, whilst in the latter it is quite linear.

REPTILIA.—The spermatozoa of the scaly Reptiles have a thickened cylindrical or fusiform head with a long tail—*Lacerta*, *Coluber* (Ecker).

AVES.—A similar form recurs in Birds. The head is either simple, cylindrical, and straight, as in the Pigeon, Heron, Gull, and the Rapacious and Climbing Birds, or it has acute edges, and is twisted spirally.

Fig. 179.

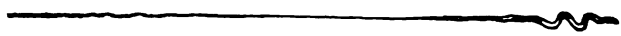

Fig. 179. Spermatozoon of a Canary.

MAMMALIA.—The spermatozoa of Mammals are so far constructed upon a common type, that they all possess a thickened capitate extremity approximating more or less to the form of a disk and a thread-like appendage or tail.

In the *Pig* the head is oval, with a recurved point, and is equally flattened on the two sides. Those of the *Bull*, *Sheep*, and *Horse* possess a similar form.

Amongst the *Rodentia*, on the other hand, the shape is very various.

In the *Rabbit* the capitate extremity is oval, flattened at the sides, and truncated where it is attached to the thread-like tail; in the *Guinea-pig* it forms an almost circular disk, that at the upper border likewise exhibits a peculiar caplike appendage.

Fig. 180.

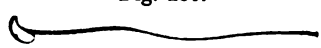

Fig. 180. Spermatozoon of the Mouse.

Those of the *Rat* and *Mouse* possess a hatchet-shaped head, the tail forming as it were the handle of the hatchet. The upper recurved extremity of the head is long and pointed in the *Rat*, shorter in the *Mouse*, and sinuous in the *Field-mouse*.

In the *Dog* the head is pyriform: in the *Cat*, oval; the tail arising from the broader side.

The head of the spermatozoa in the *Hedgehog* appears truncated below, with lateral insertion of the tail.

The spermatozoa of the *Bat* also present the form of a truncated oval, and the tail is attached to the middle of its lower border.

In the *Monkey* the head is oval, with the broader extremity towards the tail.

The spermatozoa of *Man* present an oval head, with a thickened and rounded posterior border, to which the tail is attached. The head is prolonged anteriorly into a thin disk,

Fig. 181.

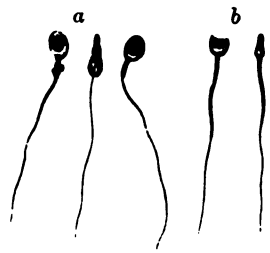

Fig. 181. Spermatozoa of Man. *a*, undeveloped; *b*, mature.

slightly depressed in the centre. Hence when seen laterally, the head appears more or less pyriform. The thickening is somewhat greater on one side than upon the other, as was pointed out to me by Leuckart. The length of the head amounts to 5 μ; the breadth, 3 μ; the greatest thickness, 1 μ. The tail is rather attenuated where it is attached to the head, enlarges to 1 μ, and then runs out to a point for a length of 50 μ.

STRUCTURE OF THE SPERMATOZOA.—Much interesting information has recently been obtained in regard to the structure of the spermatozoa.

According to Valentin,* the spermatozoa of the Bear present

* *Zeitschrift für rationelle Medicin*, 3 R., Band xviii., p. 217; and Band xxi., p. 39.

three band-like rows of roundish bodies, an anterior, a middle and a posterior. Hartnack regards these bands as elevations and depressions that reveal themselves to the eye of the observer, according to the direction of the incident light, by a play of light and shade. Valentin and Fleury depict these bands in the Bear, Rabbit and Dog. The Cat, Ram, and Guinea-pig also exhibit them, though with progressively less and less distinctness. They are seen without much difficulty with moderately powerful lenses, and I have detected them in the Dog and Rabbit with a No. 9 Hartnack.* They constitute good test objects for the microscope.

Grohe,† as the result of his careful inquiries, considers the spermatozoa to consist of two parts, a structureless investment and contractile contents, the latter being chiefly collected in the head. He regards the above-mentioned bands as due to a peculiar distribution of the contents of the body.

Schweigger-Seidel‡ so far agrees with him that he admits the existence of an external limiting membrane and contents, though he has only been able to perceive the former as a separate membrane in Amphibia and Birds.

Fig. 182.

Fig. 182. Spermatozoa of the Bat, with distinct intermediate portion.

Schweigger-Seidel distinguishes an "intermediate segment" situated between the head and tail, and demonstrates its existence in the Frog, Triton, Cock, Finch, and many Mammals. I

* *Ueber die Genese der Samenkörper*, "On the Development of the Spermatozoa." Max Schultze's *Archiv*, 1867, Band iii., Taf. xiv., Fig. 2 and 5.

† Virchow's *Archiv*, Band xxxii., p. 416.

‡ Schultze's *Archiv*, Band i., p. 309.

have already corroborated his statement in Man, the Hedgehog, Dog, Guinea-pig, Rabbit, Frog, and Triton,* and Kölliker† also concurs in its accuracy. I have not always been able in apparently mature spermatozoa to perceive the line of demarcation between the intermediate piece and the tail, and must therefore refer to an investigation of the semen obtained from the female genitals. An opportunity for pursuing this inquiry offered itself to me in a Bat that had been isolated for thirty-six hours. Both the vagina and uterus were here filled with spermatozoa in lively movement, all of which exhibited a very distinct intermediate portion. The length of this intermediate portion varies, according to Schweigger-Seidel, between 9 and 23 μ; in Man it amounts to 6 μ.

MOVEMENTS OF THE SPERMATOZOA.—As I have already remarked, in a few animals the spermatozoa are perfectly motionless, even when within the female generative organs; *ex. gr.*, Oniscus: in others we find indications of motility in the occurrence of amœboid changes of form, as in the Nematode worms (Schneider), Daphnia (Leydig), Crabs (Owsjannikow). The greater number of the different kinds of spermatozoa are, however, capable of performing a very considerable amount of locomotion. These are materially assisted by the action of the above-described undulating membranes. The movement may consist in a regular and progressive advance, as in the spermatozoa of the Canary, where the whole spermatozoon rotates extremely rapidly on its axis; or it may present a leaping or convulsive character, as in Mammals. Between these extremes there are all conceivable variations: where it is distinctly marked, the capitate extremity always goes first. Grohe believes that the movement is initiated by the contraction of the contents, which, however, with Schweigger-Seidel and Kölliker, I consider to be doubtful. I have never been able to distinguish any movements of this kind in the head, though headless tails may often be seen in lively vibration. I must also demur to the statement of Schweigger-Seidel, that the intermediate portion is rigid, and takes no part in the move-

* Max Schultze's *Archiv.* 1867, Band iii., p. 264. † *Loc. cit.*, p. 530.

ment. The duration of the movement varies considerably with the medium in which they are placed. In the body of the animal they last as long as forty-eight hours, but in the female generative organs they may be perceived even after eight days have elapsed.

Alkaline solutions act favourably in maintaining the movement, whilst acids, or the addition of a large quantity of water, act prejudicially. Concentrated solutions of certain salts, of sugar, and albumen, according to the discovery of Kölliker,* are capable of re-exciting movements in spermatozoa that have been rendered quiescent by the addition of water. Solutions of caustic potash and soda, containing from 1-32 to 50 per cent., are excitants; and woorara is a powerful irritant. Cocain (? codein), like sulphate of morphia, exhibits no action on the movements (Wagner, Kölliker, Leuckart, Mantegazza). According to the last-named author,† the spermatozoa preserve their power of movement at temperatures varying from − 15° C. to + 47° C. (= 5° to 116° Fahr.)

Frozen spermatozoa recommence to move on being thawed. They may be kept at a temperature of 0° C. (32° Fahr.) for four days without losing their motor power.

According to Kölliker, semen dried after being placed in indifferent fluids and certain saline solutions will sometimes exhibit movements in the contained spermatozoa when moistened with the same fluid or with water.

DEVELOPMENT OF THE SPERMATOZOA.—The origin of the spermatozoa has been so frequently investigated, that it is remarkable this subject has not long since been exhausted. There are, however, special difficulties in the way, dependent on the minuteness of the objects under examination, the discovery of completely indifferent fluids, and the circumstance that in the higher animals, at least, the various forms presented by the spermatozoa at different stages of development, are not very well defined. Before we enter into a consideration of their origin, it is right that we should examine the

* *Zeitschrift für wissenschaftliche Zoologie*, Band vii. p. 201.

† *Journal de l'Anatomie et de la Physiologie*, 1868, p. 184.

very various views that have been expressed in respect to their nature and significance, the rectification of which has been reserved for the present time.

Kölliker* first demonstrated that the spermatozoa were to be regarded, not as individuals possessed of independent life, but as elementary parts of the organism, and showed their origin in cells. He held that they develop in the nucleus, and subsequently in the cell, within which they for a time lie coiled up, until at length they are set free by the bursting of the latter.

Reichert† vigorously opposed the views of Kölliker, and, supported by his researches on Strongylus auricularis and Ascaris acuminata, maintained that the spermatozoa originated in elementary nucleated cells proceeding from a cell formation taking place in the entire contents of the mother cells.

Leuckart‡ gives the following account of the origin of the spermatozoa. At one time, he says, the entire sperm cell, with all its parts, is converted into a spermatozoon; at another the spermatozoon proceeds exclusively from the nucleus; and finally, at another, it originates from the contents of the sperm cells. In the latter case Leuckart explains the vesicles of evolution of the spermatic cells to be, not nuclei, as Kölliker thinks, but cells formed endogenously. The spermatic cells themselves, he believes, originate in a similar endogenous manner from the mother cells.

A more recent investigation of this point by Kölliker§ has led him to differ somewhat from his original statement, and he now thinks that the spermatozoa do not originate within, but as an outgrowth of the nucleus, though this can only be correctly stated of the Mammalia. The true sperm cells are partly extremely small cells and partly larger vesicles with many nuclei. The nuclei of these cells and vesicles undergo

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* *Beiträge zur Kenntniss der Geschlechts-verhältnisse und der Samenflüssigkeit wirbellose Thiere*, 1841. *Die Bildung der Samenfaden in Bläschen.* "Essays upon the Sexual Relations and the Spermatic Fluid of the Invertebrata," 1841. "The Formation of the Spermatozoa in Vesicles."

† Müller's *Archiv*, 1847, p. 58.

‡ *Handwörterbuch der Physiologie*, by Wagner, Band i., p. 851.

§ *Zeitschrift für wissenschaft. Zoologie*, Band vii. p. 201.

elongation and flattening. A separation is then visible between an anterior darkly contoured and a posterior somewhat smaller pale-edged portion. Thus, whilst in many instances a very small dark capitate thickening is seen at the anterior pole, a short thread-like appendage makes its appearance at the posterior, which soon forms a long tail, and at the same time the paler posterior part of the nucleus continuously diminishes in size. The fully developed zooid lies for some time longer coiled up in the mother cell, and usually frees itself by the head bursting through one part and the tail through the opposite. Fragments of the mother-cell remain attached to the spermatozoon for a little while longer, partly as a cap-like appendage, but especially adherent to the tail. Kölliker finally gives the following *résumé* of his views respecting the development of the spermatozoa throughout the animal kingdom:—

1. The fertilizing agents of all animals are developed by the direct conversion of the nuclei of the sperm cells.

2. The motionless seminal bodies of the Arachnida, Myriapods, etc., are simply modified or morphologically altered nuclei.

3. In the case of the active seminal bodies, or spermatozoa, besides the body of the zooid, a movable fibre is developed from the nucleus.

Ankermann* considers that in the Frog every spermatozoon is developed from a nucleated cell. The nucleus forms the head, whilst the tail originates in a protrusion of the cell membrane.

Pflüger† regards the spermatozoa as small ciliated cells, and refers their origin to a process of free cell formation.

Henle‡ agrees with Kölliker in believing the body of the spermatozoa in Man and Mammals to be a metamorphosed nucleus, but thinks that a persistent connection of the body with the cell is indispensable for the formation of the tail.

Grohe§ considers it to be probable that the contractile sub-

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* *Zeitschrift für wissenschaft. Zoologie*, Band viii., p. 129.

† *Ueber die Eierstöcke*, p. 93.

‡ *Handbuch der Eingeweidelehre*, p. 356.

§ *Loc. cit.*, p. 226.

stance of the spermatozoa is developed independently from the cell contents, having the same relation to it, therefore, as the sarcous elements have to the muscle cells.

According to the researches of Schweigger-Seidel, the spermatozoa are by no means simple nuclear structures, but constitute single-ciliated cells, proceeding from the metamorphosis of an entire cell.

In my first communication that appeared simultaneously with his,* I expressed myself to the effect that *not only the nuclei but the protoplasm of the seminal cells* took part in the formation of the spermatozoa, and I endeavoured to furnish a description of their development in Mammals, Birds, and Amphibia. In a second communication I added my observations on Arthropoda and Mollusks.

In accordance with the observations of Zenker † on *Asellus*, and with those of Keferstein‡ on *Helix pomatia*, I have observed the development of the spermatozoa occur with persistence of the original nucleus.

Since this date Kölliker § has again expressed his views upon the development of the spermatozoa, but finds no reason to differ from his later statements.

Owsjannikow ‖ supplies us with very interesting data upon the still little examined development of the spermatozoa in *Fish*. The testes of the *Salmonidæ* possess epithelial cells, that are usually cylindrical, and arranged in two layers. The cells present a large white nucleus, with distinct nucleoli and protoplasm. The cells of the second and third layers exhibit fission of the nucleus and protoplasm, undergo coincident increase in size, and may ultimately contain from ten to fifteen or more young daughter-cells, without losing their form. These constitute the young spermatozoa. The nucleus of the cells becomes the head, and the protoplasm surrounding it the tail.

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* Max Schultze's *Archiv*, Band i., p. 403.

† *Archiv* für N., pp. 20 and 103.

‡ *Die Classen und Ordnungen des Thierreiches*, Band iii., p. 1215.

§ *Handbuch der Gewebelehre*, p. 530.

‖ *Bulletin de l'Academie de St. Pétersbourg*, T. xiii., p. 245.

Metschnikow* communicates some important facts respecting the development of the spermatozoa, which unfortunately are inaccessible to me. According to a detailed abstract of his essay, by Hensen and Kupffer, he found sperm cells in the *Earth-worm*, with granular nuclei. The granules run together in the interior of the nucleus, and form a smooth spheroid, which elongates with the nucleus, whilst the plasma of the cell is protruded at one side to form the tail.

In the *River Crawfish* the head originates in an independent intercellular formation, that lies beside the nucleus. Moreover in *Flies* the nucleus plays no part; but the granule-heaps, from which the spermatozoa proceed, divide, and then coalesce again into a single mass. The large zooids of Cyprois develop in a similar manner, near or at the side of the nucleus.

Balbiani† also observed a body near the nucleus of the cell, which developed into the head of the spermatozoon.

I have continued my researches on the development of the spermatozoa up to a very recent period, and shall now give

Fig. 183.

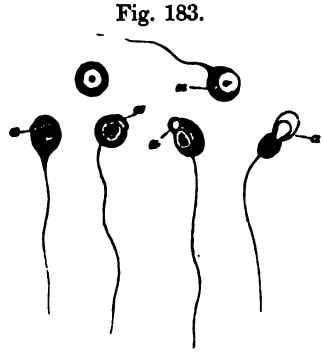

Fig. 183. Development of a spermatozoon in the Guinea-pig. *a*, head cap.

briefly my views upon the subject. I have already fully detailed the mode in which the sperm cells multiply. I regard the starting-point for the consideration of the development of

* *Mémoires de l'Academie de St. Pétersbourg*, 1868.

† *Journal de l'Anatomie et de la Physiologie*, 1868, p. 218.

the spermatozoa to be uni- or multi-nucleated cells, the nuclei of which have a granular aspect. The nucleus then becomes clear, and exhibits a peculiar change. In Guinea-pigs it contains a round nucleolus for some time, and a deposit occurs in its upper half, in the form of a nodule, that becomes expanded, and lying close to the nucleus presents in its optical transverse section the form of a signet-ring. The nucleus then elongates and projects from one side of the cell. The nucleolus has by this time vanished. From the other side the protoplasm of the cell projects to form the tail, which becomes connected with the nucleus. The cell substance, that at first enclosed the nucleus and upper part of the tail

Fig. 184.

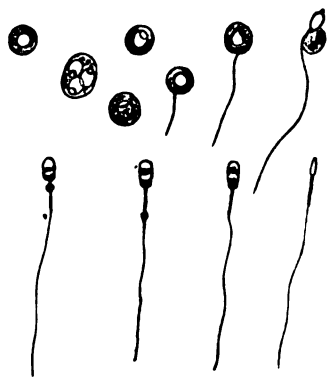

Fig. 184. Development of a spermatozoon in the Dog.

like a sac, gradually disappears as the head becomes free on the one side, and the tail upon the other, and finally remains as a larger or smaller appendage to that segment of the spermatozoon that corresponds to the intermediate portion of Schweigger-Seidel. The nodule of the nucleus becomes the cap-like appendage.

In the Dog I observed upon two occasions peculiar alterations in the nucleus. One of these was, that a vesicular body appeared at one side of the nucleus, in the other the upper half of the nucleus presented a thicker contour.

Whether the sperm cell be uni- or multi-nucleated, is a matter of no consequence, since the multi-nucleated are only to be regarded as the sum of several, the number of which corresponds to the number of the nuclei, with a certain quantity of the cell substance surrounding the nucleus.

Fig. 185.

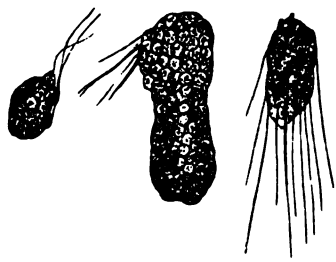

Fig. 185. From the testes of the Mouse.

Kölliker observes, " that the proof that the sperm cells play no essential part in the formation of the tails of the spermatozoa lies in the fact that very often many tails are formed in one cell." Properly speaking, each sperm zooid is developed from a special cell, but in these cases no separation takes place between the cell substance of the several cells.

Fig. 186.

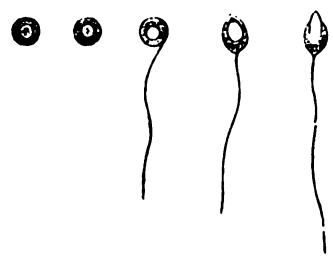

Fig. 186. Development of the spermatozoa of the Mole.

From the above statement it appears that Kölliker admits the tail to be developed in every instance from the nucleus.

I must remark, however, that I have never seen nuclei with projecting tails without cell substance, and that since I have

known the proper degree of concentration of the fluids to be applied, I have never seen coiled-up tails.

Kölliker believes that, in the formation of the tail, the nucleus, as it develops, is protruded from one pole as a delicate tube. I have frequently seen these nuclear appendages in the seminal corpuscles of the Bull, in a one-half per cent. solution of common salt, and in solutions of chromate of potash; with Henle, I regard them as the remains of the sperm cells.

Fig. 187.

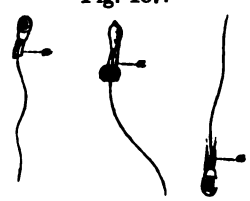

Fig. 187. Spermatozoa of the Bull, with nuclear appendage.

The development of the spermatozoa of the brown land-frog must be regarded as highly remarkable, and as quite exceptional amongst the Vertebrata. After Remak, Ankermann, and Kölliker had investigated this subject, it has recently been again examined by Neumann. It would lead us too far to

Fig. 188.

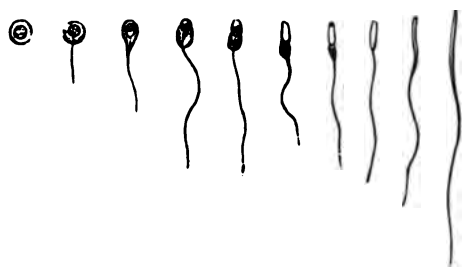

Fig. 188. Development of the spermatozoa of the Rana temporaria.

recapitulate the views that have been hitherto advanced respecting it, and I shall only give briefly the results of my own observations. The seminal corpuscles of the *Rana temporaria* develop in a manner exactly similar to those of the

Rana esculenta. Their sperm cells form spheroids, like the testicular spheroids of insects. These spheroids are enclosed in a delicate membrane, in which are several large nuclei with nucleoli. The cells, at first of large size, and few in number, with granular nuclei, increase by fission so as to form a cluster of considerable size. Each of these produces one spermatozoon; the nucleus becoming clearer, and situated at the head, whilst the cell substance is protruded to form the tail. Ultimately the membrane of the testicular spheroid bursts, and exhibits, besides the remains of the protoplasm, one or several nuclei, which, however, have nothing whatever to do with the sperm cells.

Fig. 189.

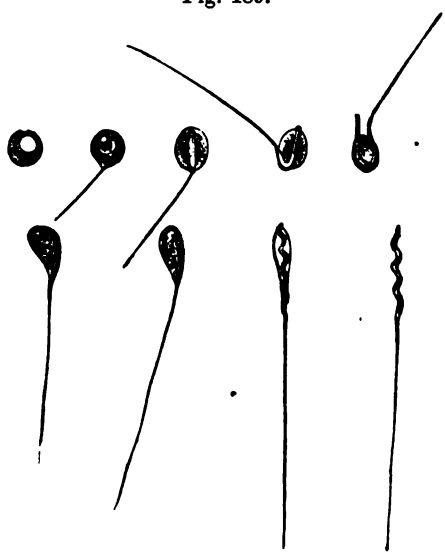

Fig. 189. Development of the spermatozoa in Raja Batis.

For the investigation of the development of the spermatozoa of the Fish, I found a very suitable object in the testes of the Skate. The formation of the seminal corpuscles appeared to commence from large cells, measuring 10 μ in diameter, which contained bright nuclei, having a diameter of 5 μ; as in the case of several Mammals, I observed a vesicular enlargement at one side of the nucleus. The nucleus then elongated, and

exhibited a kind of nodule at its anterior extremity. The tail sprouted from the opposite side of the cell, and soon formed a connection with the nucleus. The head continued to increase in length, and appeared to be curved, though still always invested by the cell. It then began to assume a spiral or corkscrew-like form. Ultimately it straightened itself out again, and exhibited a regularly shaped spiral, 34 μ in length, to which was appended a straight tail 85 μ in length.

We thus see there is complete agreement amongst all the *Vertebrata* in the development of their spermatozoa.

As regards the *Invertebrata*, my investigations are not exhaustive, but this much is certain, that in the Mollusks and Arthropods the tail in part proceeds from a lustrous body lying near the nucleus. Whether this body is a product of the fission of the nucleus or not, is doubtful. I have sometimes seen it double, and have also seen several nuclei lie near it, as well as only a granular mass from which it appeared to have

Fig. 190.

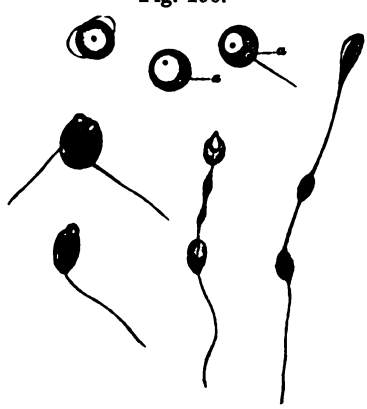

Fig. 190. Development of the spermatozoa of Helix nemoralis.

proceeded. The upper part of each tail invariably appears thickened at its origin, even when it is impossible to distinguish any peculiar body at this point in the ripe spermatozoon.

The protoplasm of the cell appears to be here also indispensable for the protrusion of the tail.

VESSELS AND NERVES OF THE TESTIS.—The bloodvessels of the testis spring from the arteria spermatica interna, and penetrate the posterior border of the gland, dividing partly in the corpus Highmorianum, and in part upon the surface of the organ, within the substance of and beneath the tunica albuginea. From both parts they enter the gland substance, and form a wide-meshed capillary plexus around the seminiferous tubules. The distribution of vessels to the epididymis, which is supplied by the arteria deferentialis, is more sparing. The veins behave like the arteries, and run upwards in the posterior part of the albuginea.

The *lymphatics* of the testis have lately been very carefully examined by Ludwig and Tomsa.* That they were remarkably developed, had already been known from the time of Panizza,† but their origin remained undiscovered. Ludwig and Tomsa have now, however, shown that the lymphatics of these glands arise from wide passages destitute of proper walls, running between the tubuli seminiferi. His‡ has corroborated these statements, and demonstrated by means of silvered preparations that the lymphatic radicles of the testis are lined by a characteristic epithelium. Frey,§ from the results of his numerous experiments with injections, also concurs in these views. Tommasi‖ treated recent sections of the testes with a 4 per cent. solution of nitrate of silver, and came to the conclusion that the lymphatics of the testis terminate in a system of lacunæ, in which the tubuli seminiferi are suspended, and that the walls of these lacunæ are invested with an epithelium analogous to that of the lymphatics, which also covers the seminiferous tubules.

Kölliker¶ assents to the accuracy of these statements. In the Bull he found the diameter of the finest tubules to be from 40 to 90 μ, whilst the epithelial cells were from 90 to 110 μ in length, and from 10 to 20 μ in breadth. He, like myself,

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* *Wiener Sitzungsberichte*, Band xliv., p. 221.
† *Osservazioni*. Pavia, 1836, Tab. viii.
‡ *Zeitschrift für wiss. Zoologie*, p. 469.
§ Virchow's *Archiv*, Band xxviii., p. 370.
‖ Virchow's *Archiv*, Band xxxviii., p. 370.
¶ *Handbuch der Gewebelehre*, p. 533.

easily satisfied himself of the presence of an epithelial investment on the tubuli seminiferi, by treatment with nitrate of silver.

As regards the *nerves* proceeding from the plexus spermaticus internus, no observer, up to a very recent time, was able to follow them to their ultimate distribution. Quite lately, however, Letzerich* has described the mode of termination of the nerves in the testes of Mammals and of Man.

In fresh seminiferous tubules, or in those that have been macerated for twenty-four hours in a solution of chromic acid, containing from 1-20th to 1-25th per cent., Letzerich saw nerve fibrils that penetrated the connective-tissue layer and membrana propria, and terminated between this membrane and the first layer of cells in a dark granular substance. The latter consisted of a granular, lustrous, and irregularly shaped mass of protoplasm, into which the nerve penetrated, ending in fresh preparations in a dull, but in slightly hardened preparations in a brightly refracting, nodule. The nerve sheath did not penetrate the protoplasmic mass, but appeared to be continuous with a membrane of extreme tenuity that invested it, so that the proper termination of the nerve fibril seemed to be formed by a relatively short and broad axis-cylinder, with usually an excentrically situated round and bright bulb.

These which, if accurate, are certainly very valuable observations, have not as yet been corroborated. I have hitherto in vain attempted to do so myself.

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* Virchow's *Archiv*, Band xlii., p. 510.

CHAPTER XXV.

OVARY AND PAROVARIUM.

By W. WALDEYER.

THE ovaries (*Eierstöcke*) are as widely distributed through the animal kingdom as the process of sexual reproduction itself. If their structural characters be in many cases of such extreme simplicity that it is scarcely possible to speak of them as special organs, the structure of the female germ is nevertheless, with perhaps the solitary exception of the Porifera, always associated with a remarkably complex arrangement of cells developed in a special region of the body, thus forming a contrast to the mode in which the buds and germs of a sexual propagation are formed.

In the ovaries the eggs are formed, and here they ripen, become invested with special protecting membranes, and often remain for years. As a general rule, the more highly developed is the entire organism, the more complex also is the structure of the ovary.

In the three highest classes of the Vertebrata, Mammals, Birds, and Reptiles, and probably also amongst the Sharks, on which, however, I have myself made no observations, the mature ovary possesses, as its essential constituents, (1) the epithelium of the ovary, or germ-epithelium; (2) the egg- or Graafian-follicles, in which (3) the ova are contained. These structures are supported and connected by an extremely vascular stroma of connective tissue, containing also muscles and nerves.

We shall, in the first instance, discuss the arrangement and

relations of the several parts just mentioned, as found in the periphery of the mature ovary of Man or other large Mammal,

Fig. 191.

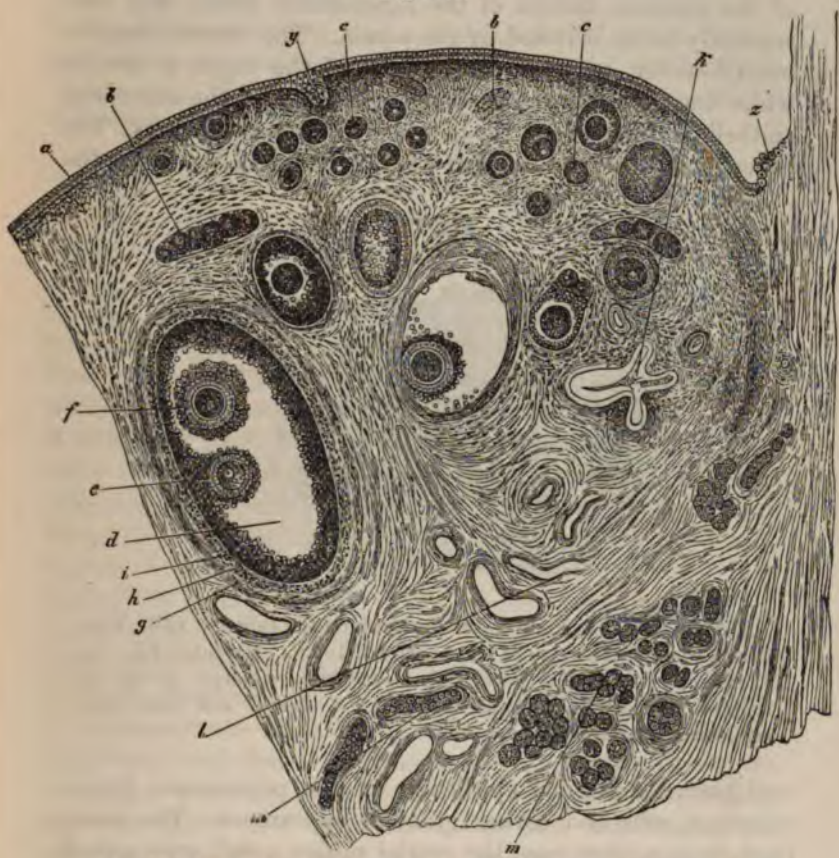

Fig. 191. From the ovarium of an old Bitch, representing a portion of a sagittal section. Hartnack 3-4. *a*, Germ epithelium ; *b b*, ovarial tubes ; *c c*, younger follicles ; *d*, older follicle ; *e*, discus proligerus, with egg ; *f*, epithelium of a second egg in the same follicle ; *g*, tunica fibrosa folliculi ; *h*, tunica propria folliculi ; *i*, epithelium of the follicle (membrana granulosa) ; *k*, collapsed, atrophied follicle ; *l*, vessels ; *m*, *m*, cell tubes of the parovarium in longitudinal and transverse section ; *y*, tubiform depression of the germ-epithelium into the ovarial tissue ; *z*, commencement of the germ-epithelium close to the lower border of the ovary.

and in the adjoining figure of a sagittal (antero-posterior) section of the ovary of an adult Dog.

The ovary appears at first sight to be enclosed in a duplication of the posterior lamina of the ligamentum latum, and consequently to be invested by the serosa. The careful observer may, however, perceive at the base of the organ a circular white line, at which the peritoneum ceases, and the superficial epithelium of the ovary, the germ-epithelium, commences. The latter (compare figs. 191 and 192) is distinguished from the

Fig. 192.

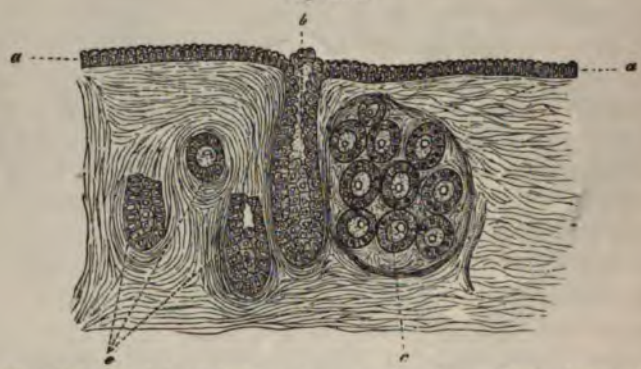

Fig. 192 (No. 14, Plate ii., of my work on the subject, 123). Vertical section of the ovary of six-month-old Bitch. Hartnack 2-7. *a*, Epithelium; *b*, ovarial tube with free orifice; *c*, larger groups of follicles arranged in a grape-like form; *e*, oblique and transverse sections of ovarial tubes.

well-known flat-celled epithelium of the peritoneum, by its columnar cells and darker granular appearance. The germ-epithelium confers upon the ovarial surface a dull grey aspect, which contrasts strongly with the bright appearance of the serosa, and resembles rather that of a mucous membrane. In any attempt to represent the peritoneum as a separate membrane it must be acknowledged to be as completely interrupted by the ovary as by the pavilion of the Fallopian tube. The similarity of these two parts, as well as the propriety of the statement that the investing epithelium of the ovary resembles the epithelium of a mucous membrane, are clearly shown by the cir-

cumstance that in a large number of ovaries the epithelium lining the Fallopian tube is continued directly into the epithelium covering the ovary, except that the cells no longer bear cilia.

The ovaries of Amphibia, Osseous Fishes, and Cyclostomata have no germ-epithelium investment, the explanation of which will be subsequently given. I have not at present been able to make any observations upon the Ganoids and Sharks.

Graafian follicles of various size are in part indistinctly visible through the superficial layers of the ovary, and partly project, in the form of translucent hemispherical elevations, to a greater or less extent beyond the general level, surrounded by, for the most part, a very narrow-meshed plexus of vessels perceptible even to the naked eye. Between these a few "corpora lutea" may be seen, which are ovisacs, in a condition of retrogression or atrophy. A vertical section, as at *a* in fig. 191, exhibits the germ-epithelium, beneath which is a layer of connective tissue, itself composed of several subordinate and decussating layers, in which are found a few ovarial tubes (*b b*), and young ovisacs (*c c*). To this succeed more mature ovisacs, some of which contain nearly ripe eggs; and lastly, the highly vascular hilus stroma, that is commonly described as *medullary substance*, in contradistinction to the above-mentioned layers that are collectively regarded as the *cortical substance*. The term *parenchymatous zone—zona parenchymatosa*—might be distinctively applied to the cortical layer; and that of *vascular zone—zona vasculosa*—to the medullary substance. The ovaries of adult Mammals, of Man, and essentially also of all Birds, Reptiles, and Sharks, are constructed on this general type. In the latter classes, and especially in Birds, the organ becomes divided on the one hand by deep constrictions into several closely applied lobules, whilst on the other, from the number and size of the mature ovisacs, which ultimately hang by short stalks from the surface, it assumes a grape-like appearance, that at first sight appears to indicate a profound distinction between them and the compact form usual in the ovaries of Mammals.

I must expressly state, however, that the above account only

holds for the mature ovary, since both in regard to form and histological structure no organ varies to a greater extent during its development and period of sexual activity than the ovary. We shall hereafter describe its various phases of development, and at present shall confine ourselves to the consideration of its characters when mature.

The greater part of the *stroma of the ovaries*, both in Man and Mammals, consists of pure connective tissue. The connective tissue of the vascular zone consists of long fibres, and is of loose texture, fibres of elastic tissue not unfrequently winding around its fasciculi. That of the parenchymatous zone of the adult female is divisible into a dense external layer, composed of short fibres decussating in various directions, and an internal layer, containing numerous cells, amongst which are the ovisacs, the larger ones projecting into the vascular zone.

The presence of a tunica albuginea, as a special tunic investing the ovary, is now admitted rather in accordance with custom than upon any real anatomical or histological evidence; certainly no true connective-tissue investment can be demonstrated by the aid of the scalpel. In Man, as has been accurately stated by Henle (50), a layer, consisting usually of three laminæ, may be demonstrated under the microscope upon the external surface of the organ, composed of rather short dense connective-tissue fibres, with a few fusiform cells distributed amongst them. These three laminæ, of which the first and third commonly run in the direction of the long axis of the ovary, whilst the middle one is transverse, may together perhaps be regarded as representing the albuginea. It is to be remarked however, that in the new-born infant, and even as far on as to the third year of life, it is impossible to distinguish a continuous fibrous investment, since ovarial tubes and Graafian follicles lie immediately beneath the epithelium, whilst, as age advances, the number of these dense strata, poor in cells, increases, so that at this period as many as five or six such layers may be discriminated; ultimately the so-called albuginea is no longer separable from the subjacent fibrous tissue passing into it without any distinct line of demarcation.

Immediately subjacent to the just-mentioned layer of parallel fibrous bands belonging to the so-called albuginea, is a layer of dense connective tissue, containing but few cells, the fibres

of which exhibit no special arrangement, but run in every direction, and are continuous internally with the stroma, which is rich in cells, and encloses the greater number of the follicles. All the connective-tissue fibres present in these peripheric layers appear dark on transverse section, like elastic fibres, whilst they are lustrous in longitudinal section. They clear up, though with difficulty, on the addition of acetic acid; but if it be desired to bring the scattered follicles rapidly into view, it is best to employ caustic soda.

The stroma of the ovary around the more deeply situated and younger follicles contains a large number of fusiform cells, with, in many instances, very long processes. Wherever the larger vascular trunks traverse this cellular layer, to reach the surface of the ovary, they are accompanied by strong fasciculi of connective tissue, which expand like an umbrella peripherically, and form trabeculæ supporting the delicate cell-containing tissue.* In animals, and especially in those whose ovulation frequently occurs, granular cells are very numerous, an indication that in this layer, in which the development and degeneration of the follicles chiefly occurs, the stroma also undergoes manifold changes. M. His (52) has demonstrated the presence in the ovary of a second kind of cell, which he has named "granule cell," and which in all points resembles the ordinary colourless blood cell. His view, however, that the follicular epithelium originates from them, as will be subsequently shown, must be regarded as erroneous.

In the mammalian ovary *smooth muscular fibres* are limited to the vascular zone that is in immediate contact with the above-described highly cellular parenchymatous zone. They lie here in detached longitudinal fasciculi, surrounding the larger and medium-sized arteries, which they sometimes invest like a sheath. See Aeby (1) and Grohe (49). They may be followed as far as to the cortical layer, but in Man at least, and our ordinary domestic animals, do not enter it; in no case does it extend to the follicular walls. The relations are somewhat different in the Amphibia and in the Osseous Fishes, fasciculi of smooth muscular tissue being here generally discoverable in

* See upon this point Henle (50), p. 481.

the larger trabeculæ of the stroma, extending between the Graafian follicles and reaching in part to the external peripheral layer. The ovaries of the osseous fishes may even have a complete muscular investment, from which numerous smaller muscular bundles radiate into the several egg-bearing lamellæ.

The question of the relations of the smooth muscular tissue in the ovaries has given occasion to a controversy, that has not as yet been in any way decided, as to whether the musculature stands in direct relation with the bursting of the follicles and the act of expulsion of the eggs. His (52), Rouget (99), Klebs (56), and Aeby (1), go the farthest, who all consider that the muscular tissue forms a large proportion of the stroma of the ovary. M. His is even of opinion that the entire interstitial tissue of the ovaries is nothing but a peculiarly modified and confused mass of muscular tissue, for which he proposes the name of "fusiform tissue." The vessels of the ovary, according to the same author, possess no tunica adventitia or media, in the proper sense of the words, but their muscular layers everywhere give off their fibres into the ovarial stroma. M. His regards the fusiform cells of the ovary as consisting collectively of such confusedly interwoven muscle-cells. Aeby (1) holds that the smooth fibre cells enter the external layer of the wall of the Graafian follicle. Rouget (99), in addition, regards the muscular fasciculi as holding a peculiar physiological relation to the vessels, and that there is here the same arrangement of the vessels, and of the muscular fasciculi accompanying them in the form of sheaths, as in the erectile tissues. And whilst Rouget associates the mechanism of erection to this combination of vessels and smooth muscular fibres, he ascribes to the ovary a capacity for erection that is especially active at the period of menstruation, and promotes the discharge of the ova. The combination of vessels with fasciculi of smooth muscular fibres is a well-known peculiarity of the erectile tissues; but at present we cannot be said to possess any direct observations on the erection of the ovaries. Pflüger (86) indeed observed direct contractions of the stroma to occur in the ovaries of the Frog upon eletrical excitation, but was unable to arrive at any positive conclusion in the case of the Rabbit. M. His (52) regards the strong curvature of the surface that occurs in fresh sections of the ovary of the Cow as a contractile phenomenon. Frey (40) expresses himself in similar terms. The results of my own investigations agree for the most part with those of Kölliker (59), Henle (50), Pflüger (84), and others, who do not ascribe to the smooth muscular tissue so

wide a distribution in the ovarial stroma as is admitted by His, Aeby, and Klebs. M. v. Winiwater (126) has recently subjected the cortical layer to a careful histological and histochemical analysis, but has been unable to demonstrate the presence in it of any smooth muscular tissue. Lastly, the smooth muscular fibres of the hilus of the ovary proceed from fasciculi that enter into the hilus of the organ from the ligamentum ovarii, and from the ligamentum latum, on which point the reader may refer to the statements of Grohe (49) and Luschka (72).

I have already alluded to the extraordinary *vascularity* of the ovary; the hilus ovarii contains a convoluted mass of large veins, which, when strongly injected, form a kind of vascular bulb, the ovarian bulb of Rouget (99). The arteries pursue the same corkscrew-like course that is characteristic of the larger trunks given off by the arteria spermatica interna and the arteria uterina. The richest capillary plexus, closely resembling the membrana Ruyschiana of the choroid, is found in the inner membrane of the follicle, and has been minutely described by M. His (53). It is not difficult to bring this very beautifully into view under the microscope, in a state of natural distension, by spreading out the wall of a small follicle whilst still fresh, but moistened with iodine-serum. According to the statements of His (52), *lymphatics* are found in the hilus ovarii; moreover wide sac-like lymphatics are here found, which invest the follicle and yellow body like a shell, and are the cause of the easy isolability of these structures; and all these spaces may be injected by simply plunging the injecting syringe into the tissues.

No precise description of the course of the *nerves* of the ovary can be at present given. Recently, in the ovaries of the Rabbit that were in the first instance frozen, and then subjected in the form of fine sections to maceration in chloride of gold, I have been able to follow delicate nerve fibres, provided only with a very thin medullary sheath, as far as to the spaces between the larger follicles; but I have not as yet been able to ascertain their mode of termination.

The disposition of the *Graafian follicles* in the ovary is not the same at all periods of life, nor in the different species of Mammals; we shall return hereafter to the consideration of the

former point when discussing the development of the ovary. In regard to certain Mammals that are frequently used for microscopic examination, it may be remarked that in the case of the Cat and of the Rabbit a layer of extremely small follicles are arranged in grape-like groups immediately beneath the so-called tunica albuginea, forming the *cortical-cell zone* of Schrön (102), or the *cortical zone* of His (52). Schrön erroneously regarded these very young follicles as ova. Follicles clustered in a similar manner also occur in the Dog (see fig. 192, *c*). In Man, the Ox, and the Pig, especially in the larger species, the follicles are situated in the above-mentioned parenchymatous and richly cellulated zone. They are more scattered in the follicular layer, the interstitial tissue between them being more strongly developed.

In a large Graafian follicle (see fig. 191, *d*) we may distinguish a connective-tissue investing membrane, the *theca folliculi* of v. Baer (2—5), which is composed of two layers, the *tunica fibrosa* of Henle (50), or outer layer, and the *tunica propria folliculi*. The *tunica propria* is lined on its inner surface, in Mammals, by stratified columnar epithelium, forming the *epithelium of the follicle*, or membrana granulosa of authors. The epithelium (see fig. 191, *i*) is collected into various-sized masses, at one or more points, according to the number of ova contained in the follicle, which project into the cavity, and constitute the *discus cumulus proligerus*, the *germ plate, disk*, or *eminence* (Keimscheibe, Keimhügel). An ovum usually lies in the middle of this discus proligerus, whilst the remainder of the follicular cavity contains a clear fluid, the *liquor folliculi*.

The *tunica fibrosa* is composed of a thin layer of ordinary fibrous connective tissue. The highly vascular *tunica propria* consists of young connective tissue, rich in cells; the cells are usually fusiform and stellate, but many are spheroidal, and resemble amœbiform cells; in these, when vermilion has been injected into the vessels, particles of the pigment may be discovered. These layers are indistinguishable in the younger follicles; the epithelial layer with the ova here simply lies in a spheroidal cavity of the stroma. Like Henle (50), I have been unable to discover the presence of a structureless basement membrane in

Mammals, either in the older follicles where it is admitted by Kölliker (59), or in the earlier periods of their formation. As the follicular epithelium lining such simple cavities of the stroma increases with the contained ovum, it constitutes a kind of irritant to the surrounding stroma, in consequence of which an increased degree of vascularity is observable around the larger follicles. The first trace of what subsequently becomes the tunica propria appears in the form of a ring of young connective-tissue cells around the epithelial layer. This ring enlarges with the increasing vascularization, and at a later period its external layers become converted into ordinary fibrillar connective tissue, and constitute the tunica fibrosa. The development of the walls of the follicles consequently appears to be immediately connected with the formation of the vessels, and it is easily conceivable that migrating or vagrant colourless cells play a certain part in the process.

The columnar cells of the follicular epithelium appear to be entirely destitute of an investing membrane; their nearly elliptical nucleus is transparent and colourless, and is situated nearly in the middle of the cell. The protoplasm, from its behaviour when lightly pressed, must possess great tenacity and extensibility, as it can be drawn out into long threads, by means of which the several cells adhere to one another. Many of the epithelial cells contain fat cells, whilst others exhibit clear bright drops resembling vacuolæ; others, again, present an irregular shrivelled form, and these may often readily be completely flattened out under a covering glass, or break up into a finely granular mass, if a moderately strong current be established under the glass. I am inclined from all this to draw the conclusion that the cells of the follicular epithelium gradually break down in the liquor folliculi, and that the products of their disintegration in great part form that fluid, which must consequently be regarded as a transudate from the blood, with epithelial cell substance in solution. Upon this point the reader is referred to the statements of Luschka (71).

The *liquor folliculi*, when fresh, is a transparent, feebly alkaline, perfectly neutral fluid, or at least becomes perfectly transparent if it

be allowed to stand for twenty-four hours, so that the *débris* of the cells may settle to the bottom. The albuminous substance it holds in solution consists, according to my investigation, exclusively of that termed paralbumen by Scherer (123).

In the discus proligerus, which indeed only exists in the Graafian follicles of Man and Mammals, we must distinguish between the epithelium of the follicle and that belonging to the ovum. The latter (fig. 191, *f*, and fig. 193, G *a*) forms an uninterrupted circlet of columnar cells around the ovum, arranged in the form of an epithelial investment to the zona pellucida. In young follicles there is no internal cavity containing fluid, the ovum with its single epithelial investment completely filling up the space. Successive layers of epithelial cells gradually appear, in which the ovum lies imbedded; it is only at a later period that a nearly semilunar space, filled with fluid, occurs at a part remote from the ovum, and which constitutes the first trace of the follicular cavity; a large collection of epithelial cells remains, surrounding the ovum, and forming the rudiment of the discus proligerus.

In regard to the position of the ovum in the follicle of the Mammalian ovary, it may be mentioned that it does not by any means appear to be constant; various inquirers, as Schrön (102) and Henle (50), have constantly found the discus proligerus near the deepest part of the follicle, where the latter is most intimately connected with the ovarian stroma, and where the supply of blood may be expected to be most free. Others, again, as Coste (33), consider that the position occupied by the discus is close beneath the most superficial part of the follicle. I have met with it occupying both situations.

In the above description of the *structure of the ovum*, those of Invertebrata may be included, since the ova of all animals are similar in their essential features, however much they may externally appear to differ.

The earliest rudiment of every ovum consists of a simple cell, with soft granular protoplasm unenclosed by a membrane, a nucleus, and a nucleolus. The peculiarities of the youngest ova, that I, with His, term "*primordial ova*," will be more minutely discussed in speaking of their development. Since

the time of Purkyné's, v. Baer's, and R. Wagner's discoveries, the protoplasm of the (primordial) ovum has been called the *vitellus* (Eidotter), or in accordance with the judicious suggestion of His, the *chief or principal yolk* (Hauptdotter).

In reference to its behaviour in the process of development, since it alone undergoes change, this yolk receives also the name of *formative yolk* (Bildungsdotter). To indicate the nucleus and nucleolus, the terms *vesicula germinativa* (Purkyné's vesicle, keimbläschen), and *macula germinativa* (Wagner's spot, Keimfleck), are commonly used.

Already, whilst it is still retained within the Graafian follicle, the primordial ovum becomes surrounded by a series of secondary formations, that are collectively to be regarded as products of the follicular epithelium. To these belong the vitelline membrane (Dotterhaut, Eihaut), or as it is usually called in the ova of Mammals, the *zona pellucida*, and the *food yolk* (Nahrungsdotter), or according to His's nomenclature, the *secondary yolk* (Nebendotter). When these last-named parts are completely formed, we have the "*ripe ovarian ovum*" before us, which now leaves its previous resting-place, the follicle, in order to descend towards the point where it becomes fertilized. During the passage of the mature ovarian ovum through the genital canal, in the greater number of animals, and especially in those in which the embryo first undergoes further development external to the maternal organism, it obtains a larger or smaller number of protecting investments, that have been satisfactorily named by Reichert, oviducal sheaths or membranes (Eileiterhüllen).

Thus it appears that in order to give a correct explanation of the various parts of the ovum, as well as to enable an accurate comparison to be made between the ova of the various classes of animals, we must distinguish between the *primordial ovum*, *the ripe ovarian ovum*, and the *ovum* after it has acquired its *oviducal investments*.

It may be here just noted that those structures that are ordinarily termed ova in the ovaries of Birds, Amphibia, Reptiles, Fishes, etc., are not really the ova, but Graafian follicles.

The investing membrane of the ovum, the zona pellucida

(fig. 193, G *b*) appears when examined with low powers as a strong perfectly transparent homogeneous lamella sharply differentiated from the yolk; when torn with needles, the contents issue in a stream, and the membrane which offers a relatively considerable resistance rolls itself back, as especially occurs in the vitellus of the Frog. The chemical characters of the zona pellucida are still not accurately known: it resists the action of acids, especially of acetic acid, and only dissolves with difficulty in alkalies. With high microscopic powers the zona pellucida of almost all animals presents a peculiar structural character first demonstrated by J. Müller (78) and Remak (96) in the vitelline membrane of the ova of Fish. It appears, in fact, to be perforated in a radial direction by numerous pores that are very distinct in the Osseous Fishes, and confer upon the membrane in these animals, when seen on the surface, a very delicate shagreened appearance.

The pores are much finer in Mammals (fig. 193, G *b*). I have not been able to discover them in the ripe ovum of Birds, though it is here very difficult to obtain sufficiently thin sections of the vitelline membrane. Microscopically the vitelline membrane of the Bird appears to be composed of a very fine close felt of fibres.

The cells of the epithelium of the ovum, of which mention has already been made (p. 174), and which occur in Mammals as a special layer of the discus proligerus, distinct from the epithelium of the follicle, lie in immediate contact with the vitellus, and are firmly adherent to it. In Birds and Reptiles the ends of the follicular epithelium that are turned towards the vitelline membrane divide into a number of very fine rods like the free border of the intestinal epithelium.

This basement membrane, or *zona radiata*, is in the above-mentioned animals the precursor of the vitelline membrane; we may obviously also regard this as a homogeneous membrane that is perforated by numerous fine fibres of the protoplasm of the follicular epithelial cells (see fig. 194). In Fishes it is indisputable that fine hair-like processes, protoplasmic fibres, proceed from the epithelial cells, and penetrate the pores of the vitelline membrane. I can especially recommend the ova of the Perch for this investigation, which exhibit two investing

membranes; the external thick one permits these characters to be very distinctly seen, whilst with sufficiently powerful lenses (1 × 1000) they may also be distinguished in the inner membrane. Pflüger (84) describes similar relations as existing in the cells of the epithelium of the ovum attached to the zona pellucida in Mammals. Leydig (68) has also given an account of similar structural arrangements in the ova of Insects, and especially in those of Timarcha tenebricosa; they have long been recognized in the ova of the Holothuriadæ and they consequently appear to be of very general occurrence.

I believe that the formation of the vitelline membrane must be ascribed to a process allied to that by which the cuticular membrane of the follicular epithelial cells is formed. In the mammalian ovum it is effected by those cells of the discus proligerus which constitute the epithelium of the ovum. The mode in which it is effected is probably that a portion of the protoplasm of the epithelial cells undergoes a cuticular transformation, whilst delicate fibres of unaltered protoplasm remain sticking into the metamorphosed mass. Reichert (95), and especially Pflüger (84), have already, in a similar manner, explained the vitelline membrane to be a product of the follicular epithelium.

Several observers, as Ransom (91) and H. Meyer (76), have described a second very fine membrane within the zona pellucida, and in immediate contact with the yolk, occurring especially in Mammals and in Fish. This would constitute the vitelline membrane, in the strict sense of the word. I must observe, however, that I have not hitherto been successful in discovering this membrane, and Bischoff (17, 18) has directly denied its existence. Besides the pores the zona pellucida of many animals present a remarkably large opening leading to the yolk, which constitutes the *micropyle* of Keber (55). This has been very clearly demonstrated in the ova of many invertebrate animals, and especially in Insects. It has also been shown to exist in Fishes by Bruch (25) and Reichert (93). In Insects the surface of the ovum in the immediate vicinity of the micropyle often presents the most delicate sculpture, in consequence of which it projects to some extent. See in particular the description given by Leuckart (66).

In Fishes also certain appendages may be sometimes seen arranged

around the micropyle, like those, for example, that have been shown by Buchholz to exist in the Osmerus eperlanus. In Insects they arise at the point where the cell of the ovum communicates with the so-called germ yolk-cells (see *infra* and fig. 195). Pflüger (84) has given a description of larger openings in the ova of the Cat that are occupied by one of the cells of the discus proligerus, half lying within the zona, and half externally amongst the epithelium of the ovum—twin cells or plug cells (spundzellen) of Pflüger; in other cases he saw processes of the cells of the epithelium of the ovum sticking deeply in the zona pellucida. Up to the present time these observations have not been corroborated by others. Where a micropyle is present, it would appear to be constantly subservient to the passage of the spermatozoa into the interior of the ovum.

The *principal yolk* presents characters differing from those of ordinary cell protoplasm. The possession of contractile power has been recently observed in it by Pflüger (84), v. la Valette (117), and Stricker (114). It is remarkable that, with the exception perhaps of many ganglion cells, the ovum, quite independently of the secondary yolk, presents the greatest accumulation of cell protoplasm around a single nucleus with which we are acquainted; in other words, the cells of the ovum are amongst the largest uni-nucleated cells known. The protoplasm of the egg, when fresh, is very rich in granules. M. His (53) describes the protoplasm as containing numerous small granules that from their reaction appear to contain protagon, and have been termed by him *true* yolk granules, in contradistinction to the granular bodies of the secondary yolk. In young mammalian ova, granules of almost every variety of size are met with. The largest (fig. 193, G *e*) are completely spherical vesicles, and resemble the yolk spheroids of Birds; they lie scattered, as represented in the figure, between the smaller granules, amongst which they are directly visible. At a later period they increase in number, and have so strong a lustre that scarcely anything else can be seen within the zona pellucida. Their microchemical reactions agree with those of the albuminous compounds.

The germinal vesicle appears as a sharply defined globular and somewhat excentrically placed body, situated within the

principal yolk, refracting light strongly, and of large size in proportion to the cell. These large highly refractile nuclei give a very characteristic appearance, recognizable at first sight, to

Fig. 193.

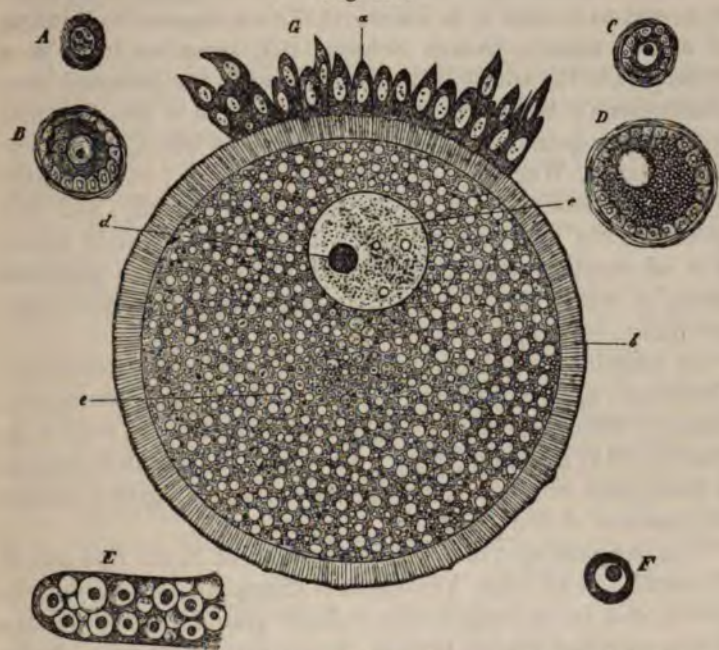

Fig. 193. A, Primordial egg of Man, from a fœtus at the eighth month (Hartnack 2-9); B, primordial follicle from a Rabbit; C, primordial follicle from a Pigeon; D, a somewhat older follicle from the same animal, exhibiting the commencement of the formation of the secondary yolk; E, cæcal extremity of the ovary of the Ascaris nigro-venosa, exhibiting germinal vesicles (in part with germinal spot and Schrön's "granule") in a diffused mass of protoplasm; F, an egg of the Ascaris nigro-venosa, from about the middle of the ovary, exhibiting Schrön's granule and the commencement of the deposit of a yolk; G, an egg from a follicle of a Rabbit, two millimeters in thickness; *a*, epithelium of the ovum; *b*, radially striated zona pellucida; *c*, germinal vesicle; *d*, germinal spot; *e*, yolk. (B—G, Hartnack 3-9.)

the cells of the ovum. Up to the present time I have never seen more than one nucleus in each cell of the ovum. Kölliker,

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however, depicts a young cell of the ovum with two nuclei; but in the ripe ovum a double germinal vesicle does not appear to have been at any time observed.

The *nucleolus*, or *macula germinativa*, is never absent in the primordial egg. It has a dull or finely granular appearance, and as I, with v. la Valette (117), am disposed to think, is of a solid nature; though Schrön (103) considers it to be a vesicle. On the addition of distilled water, the germinal spot disappears (v. la Valette, 117). The presence of two germinal spots in one germinal vesicle has often been noted, as, for example, by R. Wagner (130), in the Cockchafer; subsequently by v. la Valette (117) in the larva of the Dragonfly, and still more recently by Claparède (131), in the Earthworm, in which it is of constant occurrence. In this case the two germinal spots, of which one is constantly much larger than the other, are united to form a twin spot.

In addition to the germinal spot, a few small round corpuscles are sometimes found in the germinal vesicle, the significance of which has not as yet been ascertained. If, with v. la Valette (117) and Pflüger (84), we regard the germinal spot as a precipitate from the germinal vesicle, we may give a similar explanation of their nature.

The germinal spot only remains persistent in the ripe ova of Mammals; in all other Vertebrata it disappears at a very early period, and in its stead a cloudy finely granular mass appears in the germinal vesicle, through which several bright globules are distributed, especially in Batrachia and Fishes. The period at which the germinal spot disappears cannot be precisely fixed.

Schrön has recently described a still smaller bright and apparently solid body within the germinal spot, to which he has given the name of "Granule" (Korn). I have not hitherto been able to discover it in Mammals, but it is constant in many of the lower animals, as, for example, in the Ascaridæ, though here perhaps it may turn out to be the smaller part of Claparède's twin spot (see fig. 193, E and F). V. la Valette (117) considers the granule of Schrön to be a vacuole, and does not find it to be of constant occurrence. Balbiani (9) differs most widely in his views on this point from the others. He describes

contractile vacuoles as existing in the interior of the likewise contractile germinal spot. From the germinal spot a hollow tubular process is given off, which is lodged in a similar canal of the germinal vesicle. The vacuoles of the germinal spot communicate also with its tubular process.

It has hitherto been generally accepted, that the ripe mammalian ovum is nothing but a much-enlarged primordial ovum; recent observations and opinions, with which I fully agree, permit us to hold, with great probability, that in the ripe mammalian ovum, besides the principal yolk, a certain quantity of secondary yolk is also present. Pflüger (84) has in particular pointed out that there are two different constituents of the yolk in the mammalian ovum, of which one, that in young ova is the clearest, immediately surrounds the germinal vesicle; whilst the other is darker, and constitutes a superficial investment to the former. We may easily conceive this peripherically situated portion of yolk to be a subsequent or secondary formation, and that it may, perhaps, proceed from the follicular epithelium. This circumstance is at any rate of the greatest importance in the consideration of the comparative anatomy of the ovum. The ovum of *Birds* and of *Reptiles* has, up to the present time, occupied to far too great an extent the attention of observers in regard to the significance of its several parts. Very superficial observation shows to us that in the ripe ovarian ovum, invested by the vitelline membrane, there is a yellow mass of considerable size, *the yellow food yolk*, which is invested by a thin coating of white yolk, *the white food yolk*.

In the natural condition of equipoise of the egg when at rest, a whitish spot, from three to four millimeters in diameter, is constantly to be found at the uppermost part, immediately beneath the vitelline membrane. (See J. Oellacher, 132.) This *tread* or *cicatricula* is the germ or principal yolk with the germinal vesicle. If we examine it in the egg after it has been laid, and has been, as usual, fecundated, it will be found to have already undergone change, and we have before us the *furrowed germinal disk*. The white yolk everywhere surrounds the principal yolk, and penetrates at one point as a small thread into the interior of the yellow yolk, at

the centre of which it forms an enlargement, of the size of a pea, the *Latebra* or yolk cavity of Purkyné.*

The principal yolk with its germinal vesicle, independently of its size and the early disappearance of the germinal spots, presents no special peculiarities; it represents the primordial ovum. The chief difficulty in regard to the egg of the Bird lies in the question of the origin of the food yolk, and its relation to the primordial cell of the ovum.

In regard to the historical aspect of this matter it may here be briefly remarked that since the discovery of the mammalian ovum by v. Baer, two opposite views have been held in regard to the egg of the Bird; of these, one, supported by Schwann (104), Gegenbaur (43), Leuckart, Kölliker (58), Cramer (34), regards the whole egg of the Bird as a single cell; whilst the other, held by H. Meckel (73), Allen Thompson (115), Ecker (37), Stricker (114), His (53), and others, considers both the food yolk and the vitelline membrane to be secondary formations, and, in fact, as products of the follicular epithelium. Another controversy again has arisen in reference to the nature of the elements of the food yolk. Schwann (104) and Klebs (56), and more recently His (53), contending that they are cells, whilst others, especially Gegenbaur (43) and Stricker (114), hold them to be spheroidal bodies of peculiar nature, which have no claim to the dignity of a cell, but may rather be associated with such colloidal drops or albuminoid particles as are found in secretions.

The egg of the Bird, in its earliest state, is exactly like that of the Mammal (see fig. 193, B C D), except that the follicular epithelium always remains as a single layer, which I may mention in opposition to the statement of His (53). An increase in the contents of the follicles may soon be observed; a fluid analogous to the liquor folliculi is, however, never produced, but a finely granular mass that is deposited around the principal yolk, from which it can be clearly distinguished. This is the first rudiment of the secondary yolk mass; the principal yolk in the meanwhile remains essentially unaltered. As the follicle advances in age, the small granules of the secondary yolk aug-

* The term "cavity" refers to the fact that in the boiled egg this spherical white mass of the yolk does not usually coagulate, but remains fluid, which gave rise to the idea that there was a cavity filled with fluid.

ment in size, soon assume the form of bright polygonal bodies, and then of small spheroids of thoroughly homogeneous appearance, in which no cell membrane can be demonstrated; for the membrane that appears on the larger spheroids after the addition of water can scarcely be regarded as the equivalent of a cell membrane. These small polygonal and round vitelline corpuscles are very resistant; when flattened with the covering glass, they exhibit a stellate, streaky, fractured surface, and their reactions, that have recently been studied by His, show that they belong to the protagon-containing class of substances. Ultimately these spheroids attain very extraordinary dimensions; but we may trace the passage of the smallest corpuscles step by step into the largest. In the interior of larger spheroids one or more of the smaller corpuscles may be constantly found, and within these, again, are frequently others of still smaller size. M. His (53) rests upon this fact his view that the vitelline spheres are cells, whilst the corpuscles enclosed in them are nuclei and nucleoli. Nevertheless, their form, their instability, their firm consistence, the gradual passage of the smaller into the larger spheroids, the circumstance that as the follicles advance to maturity the number of small spheroids diminishes, whilst the larger increase, all concur to make me disagree with His's interpretation. Nor am I more disposed to concur with Gegenbaur in believing that an endogenous development of the smaller spheroids takes place in the interior of the larger. I think it is more probable that the smaller spheroids are simply forced into the interior of the larger, since the latter are of much softer consistence; whilst in every movement of the yolk the closely compacted elements of which it consists must be subjected to mutual pressure. The larger spheroids seem to proceed from the smaller by a simple process of imbibition of fluid. V. Wittich (128) has arrived at similar conclusions in respect to the ova of the Arachnida; the spheroids of the yolk are here not true cells, and they enlarge in consequence of the imbibition of the surrounding fluid albuminous substance. The yellow yolk, which subsequently constitutes the principal mass of the egg of the Reptile and of the Bird, is only a modification of the white; and he describes in particular the larger vitelline

spheroids, the mass of which is cloudy from the presence of fine molecules; how these originate, however, has not hitherto been investigated.

From whence then, in the last place, proceeds this originally finely granular secondary vitelline mass? It is incontestably a product of the follicular epithelium, and, in fact, results directly from a metamorphosis of the follicular epithelial cells. On this point I differ from Gegenbaur, with whose views I am otherwise for the most part in accordance; for Gegenbaur (45) has very recently advanced again his earlier view, to the effect that the

Fig. 194.

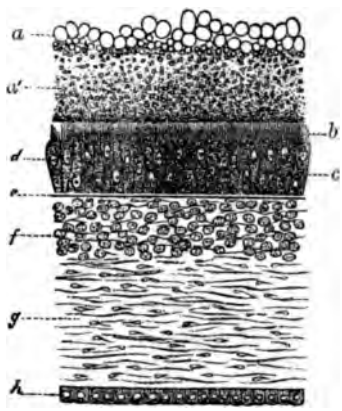

Fig. 194 (corresponding to No. 25, Pl. iii., of my book). Section of the wall of the follicle of a Fowl that had a diameter of four millimeters. (Hartnack 3-7.) *a*, Yolk spheroids; *a'* molecular vitelline layer; *b*, zona radiata; *c*, follicular epithelium; *d*, epithelial cells with fine cilia at the basal extremity; *e*, membrana propria folliculi; *f*, internal layer of the connective-tissue wall of the follicle, with numerous cells; *g*, external layer; *h*, epithelium of the ovary.

constituents of the vitellus only result from the differentiation of the protoplasm of the primitive cells of the ovum. In young ova, indeed, no difference can be perceived between the protoplasm of the epithelial cells and the finely granular secondary yolk; it appears as if the protoplasm itself issued forth from the internal membraneless extremity of the cells, and was continuous with the secondary yolk mass; whilst at the nuclear

extremity of the epithelial cells which is situated nearer to the follicular wall, new protoplasm is constantly being formed, and forced onwards. However this may be, two circumstances show that the follicular epithelium stands in immediate relation to the formation of the secondary yolk. In the first place, very small bright structures, resembling the youngest vitelline granules, are already found, especially in Lizards, in the protoplasm of the epithelial cells, and secondly, the epithelial cells of the follicle (fig. 194) are most strongly developed during the period that the formation of the yolk is taking place with the greatest activity. Meckel, v. Hemsbach (73), Allen Thomson (115), and others, have taken the same view. The radially striated layer, situated (fig. 194) between the follicular epithelium and the yolk, can form no obstacle to this mode of formation, since, as I have already shown, it is perforated with numerous pores, in which fine fibres of the protoplasm of the epithelial cells are lodged.

The ova of the *Selachia* exhibit very similar characters, as has been especially demonstrated by the researches of Gegenbaur (43). I find also that this may be said in regard to the formation of the ova in the *Osseous Fishes* and the higher Crustacea, as, for example, the Astacus fluviatilis, in which the vitelline lamellæ and vitelline spheres originate in exactly the same mode, and in the ova of which a principal and secondary yolk, like those of the Bird, may be clearly distinguished. As showing the complete and thorough difference existing between the principal and the secondary yolk, Stricker (114) has made an interesting observation in the ovum of Forella, in which, under favourable circumstances, amœboid movements can be observed in the former, whilst the latter remains perfectly passive.

The ova of the *Batrachia*, though they otherwise closely resemble those of the Osseous Fishes, do not permit a clear distinction to be perceived between the principal and the secondary yolk; in this respect they rather resèmble those of Mammals. Still many circumstances, as, for example, the presence of vitelline lamellæ, which are quite similar to those of fishes, show that here also a secondary vitelline mass is formed from the follicular epithelium, which cannot so easily

be distinguished by the eye from the principal yolk mass. I shall return to the objections which may be raised to this view from a consideration of the total cleavage undergone by the Batrachian ova.

The *vitelline lamellæ* just mentioned, found in the ova of the Chelonia, Batrachia, Cartilaginous Fishes, and of many Osseous Fishes, are doubly refractile crystals (Radlkofer) of an albuminous substance, that Kühne, in his "Physiological Chemistry," p. 552, has stated to be vitellin. Virchow (119) first established their albuminous nature by their microchemical reactions, and showed that they at least do not consist of fat, as had been previously held. The form of the crystal varies in different species, being four-sided plates, frequently with produced angles, in the Frog, whilst in the Perch very various forms occur, that for the most part change into spheres in the mature ovum. (See Radlkofer, 113).

I will add to these remarks on the ova of Vertebrata a few words on the ovaries and ova of the Invertebrata. The observations of Lieberkühn (69) on the Porifera, those of Balbiani (8) and Stein (110) on the Infusoria, and those of Greeff (48) and Strethill Wright (112, 113) upon the Rhizopods, have furnished us with some information on the uniform and remarkable relations occurring amongst the PROTOZA, though our knowledge in regard to them is still extremely imperfect.

The ova of the *Porifera* are not developed in special organs, but the several epithelial cells (?) of the walls of the system of canals traversing the sponge mass are capable of developing into ova.

In the *Infusoria*, according to Balbiani, a female organ first occurs as a special structure in the form of the so-called *nucleus*. This varies much in shape, being round, oval, or even band-like; its granular contents, which resemble protoplasm, in the act of conjugation of two infusory animalcules which precedes fertilization, divides into several portions by a kind of cleavage, and it is still questionable whether we must regard the nucleus as a single ovum, or these products of cleavage as ova, and the nucleus consequently as an ovarium, which must then consist simply of germinal matter without any tissue-forming intermediate substance.

Our information is most incomplete in regard to the female organ of the *Rhizopoda*. The few statements made by the above-named authors lead us to suppose that the structure that here contains the eggs is similar to the nucleus of the Infusoria.

The CŒLENTERATA everywhere exhibit special organs for the production of the ova, which in the higher orders, as in the Actinia, Ctenophora, etc., have a follicular form. The ova are believed to originate from the cells lining the follicles. As a general rule the capsules of the ova appear as appendages of the gastro-vascular apparatus, and in many instances as protrusions of the latter; for, as is well known, in these animals the generative products are discharged into the gastric cavity, or into the canals that radiate from it.

The ovaries of the ECHINODERMATA are composed of rounded or elongated tubes that are usually united together into several gland-like groups, corresponding in their number and arrangement with the radial segments of the body. In the higher forms, as, for example, in the Holothuriadæ (see Selenka, 105), the small gland tubes open into one or more excretory ducts. The ova lie closely compressed in the gland tubes; their mode of development, however, still requires investigation. When mature, they possess a thick vitelline membrane, that exhibits a radial striation and an aperture that is to be regarded as a micropyle (see page 177).

As regards the ovaries of VERMES, I may refer to the investigations of Meissner (75), Bischoff (134), Munk (81), Leuckart (67), Hering (51), Claparède (27, 28), and others, as well as to my own researches on the Ascaridæ, from which the following conclusions may be drawn. The true ovary is either a vesicular organ opening by a special excretory duct into the complicated sexual canal, or, as in the Ascaridæ, it consitutes the ultimate cæcal extremity of the genital tube. But since in many Vermes, and especially in the parasitic forms, such as the Cestodes and Trematodes, special glands are also present, which, since the time of Siebold, have been termed yolk-stocks ("vitelligène," "dotterstöcke"), we must here distinguish the ovary proper by the term "germ-stock" ("germigène," "keimstock"). As regards the function of these two glandular organs, which

are both obviously subservient to the development of ova, it is certain that the germinal vesicle and germinal spot are formed by the germ-stock; but in addition, as Bischoff has observed, a quantity, though often small, of finely granular protoplasm lies around and between the germinal vesicles even at the extremity of the germ-stock, and the nearer the ova approximate the excretory duct of the germ-stock, the more distinctly visible is the protoplasmic area surrounding each germinal vesicle, and each ovum comes to present the appearance of a complete cell, composed of protoplasm (or yolk), a nucleus, and a nucleolus; the ova, therefore, of the germ-stock are comparable with the primordial ova of Vertebrata. It is generally stated that in the germ-stock the germinal vesicles are alone developed, and that the whole of the protoplasm constituting the vitellus proceeds from the yolk-stock. I cannot, however, coincide with this view, and hold, with Gegenbaur (45, p. 287), that a fine investment of protoplasm surrounds each ovum as it leaves the germinal area. Moreover the morphological significance of the yolk-stocks is by no means certainly established. Gegenbaur (45) expresses the opinion that they are "parts of an extensive ovarium, of which only the smallest portion remains persistent, the greatest portion, on the other hand, degenerating to form the yolk-stocks." However this may be, it is certain that ripe completely formed cells, comparable to the primordial ova of the Vertebrata, originate in the germ-stock, or true ovarium. The researches of Stieda (135), G. Walter (124), and Leuckart (67), which I am able to corroborate from observations made on the Ascaris nigrovenosa, show that the ova themselves proceed from the epithelial cells of the ovarian tube. At any rate the most various transitional forms may be found, and at the distal extremity of the ovary the youngest ova and epithelial cells can no longer be distinguished from each other. And so we find in the Ascaridæ, that as the ova press forward in the genital tube the granular yolk-mass surrounding each germinal vesicle augments in quantity, and at a later period acquires a thicker or thinner vitelline membrane. The increase in the granular yolk, as is shown both by Leuckart's (67) observations and my own, is attributable to the epithelium investing this part of the genital tube. I must

here limit myself to these few remarks, in which I have endeavoured to point out the principal points of comparison between the ova of these animals and those of the higher classes. I am unable to enter into any details respecting the various forms of the ovaries, and the relations of their several excretory ducts, in the very numerous subdivisions, of the Vermes.

All the MOLLUSCA possess well-developed glandular organs for the formation of the ova, consisting of numerous acinous follicles, the epithelial cells of which undergo development into ova. A peculiar gland, called the hermaphrodite, is widely distributed through the class, in which, and sometimes even in the same follicles, both ova and seminal corpuscles are found, which, as Eisig (136) has very recently described in the case of the Lymnæus auricularis, proceed from the epithelial cells lining the glandular follicles. Both sexual products are consequently discharged through the same excretory duct. In Helix and Limax, so far as I have been able to see, the larger ova that are adherent to the parietes of the acini are separated from the remaining cells by a special thin-walled capsule. I have not been successful in tracing out the precise mode in which these capsules are developed, nor have I been able to demonstrate the development of an epithelium on their inner surface, by the presence of which these capsules are rendered completely analogous to the Graafian follicle of a vertebrate animal. For information respecting the development of the ova in Mollusca, I must refer the reader to the works of Semper (106), Claparède (29), Baudelot (11), Eisig, and others.

In the ARTHROPODA, which, in my opinion, stand next to the Vertebrata in the development of their female generative organs, structures may be demonstrated that precisely correspond to the Graafian follicles.

Fig. 195 exhibits in a semi-diagrammatic manner a portion of the ovarian tubes of the vanessa urticæ. The narrower portion (a) is the terminal portion of the long tubular ovary that is connected to the dorsal vessel by a delicate ligament (g). Occupying the interior of the extremity of this at a^1, just as in the ovarian tubes of the Ascaridæ, transparent germinal vesicles, with nucleoli, are found imbedded in a diffused and delicate

mass of protoplasm; further downwards we see some of these attached to the walls of the tube as epithelial cells, whilst

Fig. 195.

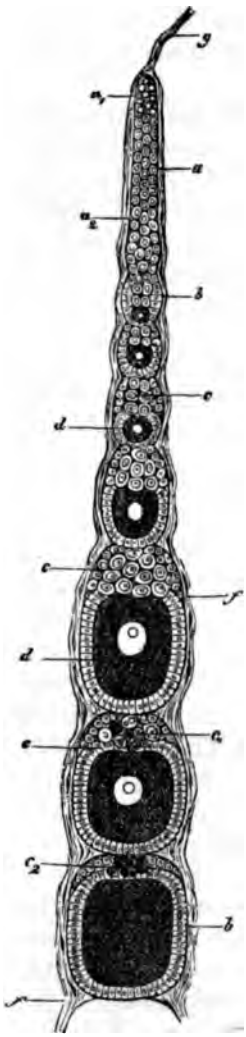

Fig. 195. Ovarian tube of the Vanessa urticæ (semi-diagrammatic); a large portion of the follicle has been removed, in order that the various stages of development of the ova may be exhibited in a single figure. *a*, Cæcal tubular termination of the ovary, containing at a^1 germinal vesicles distributed through a diffused mass of protoplasm, and at a^2 completely developed cells; *b b*, ovarian follicles; *c c*, yolk-forming cells, which are undergoing disintegration at c^1; c^2, granular mass formed of the disintegrated yolk cells; *d d*, ova; *e*, point where the micropyle subsequently appears; *f*, external wall of the ovarian tube, composed of connective tissue; *g*, process of the latter, connecting it with the dorsal vessels. Magnified about 100 diameters.

others of exactly the same size and structure occupy the lumen of the tube, as at a^2 in the figure. Still lower down, some, both

of the laterally attached and axial cells become conspicuous on account partly of their size, but especially their large and lustrous nuclei. These gradually come to occupy more and more the axis of the tube, and are enclosed in groups of from six to eight in moniliform dilatations of the tubular wall. We now also find segments of the ovarian tubes, as at *b*, in the centre of which are numbers of primordial egg cells (ova), whilst the parietal cells distinctly assume the characters of an epithelial lining to the follicles; for as follicles the several segments of the moniliform tube must now be regarded. Still lower down, however, a structural change occurs; for one of the egg cells, and always that which lies the lowest, becomes considerably enlarged, preserves it nucleus, which also undergoes great increase, and at the same time its protoplasm becomes darker, whilst the nuclei of the other primordial egg cells diminish in size, and ultimately, with their cell-protoplasm, undergo granular degeneration. Coincidentally with this the larger egg cells are separated from each other by an inflection of the epithelium, The two portions of the follicles originating in this manner are commonly distinguished as the vitelline cavity and the germ cavity; whilst, after Lubbock, with whom most recent writers are in accordance, the upper confused mass of egg cells have been called yolk-forming cells, because it has been supposed that these cells furnish the yolk of the completely formed egg cells. The existence of a cord-like structure that, in many Arthropoda, as, for example, in the Coccidæ (Claus, 30), connects the yolk-forming cells with the egg cells supports this view. I cannot, however, accept it; for I have constantly found evidences of fatty degeneration and of disintegration in the yolk-forming cells, whilst the yolk-mass of the definitive egg still continues to augment, long after those cells have disappeared. I therefore regard the yolk-mass to be, in great part at least, only a product of the follicular epithelium, to which also the vitelline membrane, that in Insects often exhibits very delicate sculpture, must owe its origin. The micropyle is formed at that pole of the egg that is turned towards the yolk cavity (see fig. 195). The structure of the ovaries in the majority of Insects, so far as we have learnt from the investigations of Stein (137), H. Meyer (77), Weismann (125), Claus (30),

Leydig (68), Lubbock (70), Landois (62, 63), Bessels (14), and others, is similar to that of the Vanessa urticæ.

I have already stated that the ova of the higher CRUSTACEA are developed in special follicles, whilst in the lower orders the ovaries are simple saccules and tubules. The ovaries and ova of the ARACHNIDA, respecting which we have very full details in the essays of v. Wittich (127, 128), present some peculiarities. The follicles are formed by lateral protrusions of the tubular ovary, and, according to the above author, possess an epithelial lining in the short cervical portion that connects them with the ovarian tube; at a later period the yolk molecules accumulate in this part of the follicle. In the first instance no germ spot can be seen in the germ vesicle; but, as is shown in the illustrations given by v. Wittich, a thin investing layer of protoplasm is constantly present. At first the vesicles lie in close contact with the walls of the ovarian tube, which, by their own enlargement and the increase of the layer of protoplasm surrounding them, they cause to protrude laterally, and thus lead to the formation of the follicles. We may here also, in all probability, regard the primordial eggs as simply enlarged epithelial cells of the ovarian tube. (Compare A in fig. 192 with v. Wittich.) A remarkable spherical concentrically laminated body, the so-called vitelline nucleus, has been discovered by v. Wittich to be, in addition to the germ vesicle, constantly present in the ova of some species of Araneidæ, it is probably identical with the similarly named body found in the ova of Batrachia and Osseous Fishes. In the Batrachia the yolk nucleus disappears in mature ova (Allen Thomson), and in the Araneidæ the central part of this body becomes fluid, whilst the peripheric remains as a capsule of firm consistence. The significance of the yolk nucleus is at present unknown.

DEVELOPMENT OF THE OVARIES AND OF THE OVA.—The first traces of the sperm or germ organ, according to the sex, in the embryo of the Fowl appears about the end of the fourth day. At this time the Wolffian body is invested with a regular columnar epithelium, whilst the rest of the peritoneal cavity is lined by small flattened cells.

From the labours of Schenk (101) we know that in the first instance the whole pleuro-peritoneal fissure is lined on its inner surface by columnar cells proceeding from the separated lateral parts of the middle germinal layer. Schenk is of opinion that this layer of cells, corresponding to the cutaneous and interstitial fibrous layer, is applied simply and exclusively to the production of the later appearing *epithelium* of the peritoneum. Götte has recently expressed himself in favour of this view in regard to the Batrachia. These columnar cells soon disappear over the greater part of the peritoneal cavity, being replaced by pale quite flat elements, the median angle alone corresponding to the middle plate of Remak, and subsequently to the Wolffian body which appears at this spot, retaining its columnar epithelial covering.

About the fourth day a considerable thickening of the above-mentioned epithelium occurs both on the median and on the lateral side of the Wolffian body; the thickening on the median side is the first rudiment of the ovary, the lateral goes to form the subsequently appearing tube called Müller's duct.

In the male embryo the thickening of the epithelium appears first in the situation of the sperm gland, but disappears again about the eighth or ninth day; whilst it continues to increase in the female.

In a short time a small outgrowth, rich in cells, projects from the interstitial tissue of the Wolffian body beneath the epithelial thickening (see fig. 196). *The thickened epithelium investing this outgrowth gradually forms the rudiment of the Graafian follicles and ova, and of the subsequently appearing epithelium of the ovary,* whilst the outgrowth itself is destined to furnish the vascular stroma of the ovary.

As soon even as the fourth or fifth day of incubation the interesting observation may be made in the embryoes of fowls, that some amongst the epithelial cells have become conspicuous by their round form, their size, and the large nucleus they contain (see fig. 196, *o*). We may conclude from the regular arrangement of these structures, and the constancy of their position, that they represent the youngest primordial ova, which thus, even during embryonic life, are formed by a simple

process of growth from the epithelial cells of the germ organ. Similar relations may be likewise easily demonstrated in Mammals (embryoes of Dogs and Rabbits).

Fig. 196.

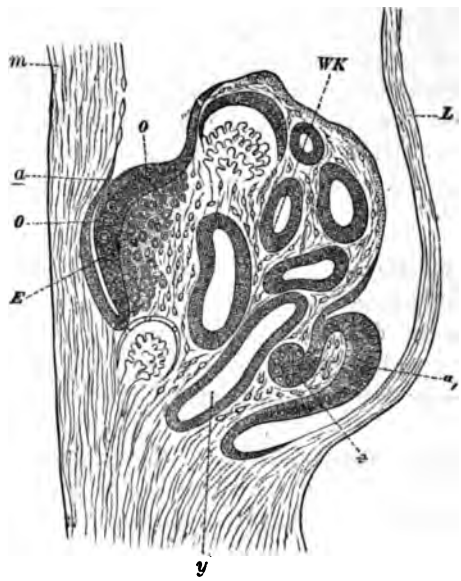

Fig. 196. (Fig. 50, Pl. v., of my Treatise.) Transverse section of the Wolffian body, with the rudiment of the ovary and of Müller's duct, taken from the embryo of the Fowl at the end of the fourth day of incubation. WK, Wolffian body; *y*, transverse section of the Wolffian duct; *a*, and *a*, thickened germ epithelium; *z*, Müller's duct in connection with the germ epithelium; E, rudiment of the ovary, with greatly thickened germ epithelium; *o o*, primordial ova; *m*, mesentery; L, lateral wall of the belly.

The further development of the ovaries depends upon a peculiar mode of growth of the superficial epithelium (germ-epithelium) on the one hand, and of the subjacent vascularized stroma on the other, of which fig 197 may be taken as a representation. Certain more or less delicate and vascular processes of connective tissue now shoot forth from the stroma, whilst coincidently the epithelium increases by the continual production of new cells; the processes then penetrate between the

epithelial cells, enclosing a variable number of them, which thus by degrees come to be more or less deeply imbedded in the vascular stroma. At *c*, fig. 197, such shoots of the connective tissue are seen, and at *d d* epithelial cells either imbedded or in process of becoming so. From the plan and mode in which these changes take place it is evident that the several epithelial masses must be connected with each other in a plexiform fashion, and consequently that the ovary at this period is composed of a framework of vascular connective tissue, the meshes of

Fig. 197.

Fig. 197. (Fig. 11, Plate ii., of my Treatise.) Vertical section of the ovary of a human fœtus at the thirty-second week. (Hartnack 2-7.) *a a*, Epithelium ; *b b*, youngest egg cells lying in an epithelial stratum ; *c*, connective-tissue trabeculæ that project into the epithelial layer ; *e e*, primordial follicle, with an investment of small connective-tissue cells ; *f*, groups of epithelial cells (egg balls) that have already become imbedded, with a few subjacent and larger cells (primordial eggs) ; *g*, granule cells of M. His.

which communicate freely as in a cavernous tissue. M. His (52) and Kölliker (59) have already called attention to the peculiar cavernous structure of the fœtal ovary, though undoubtedly without recognizing the mode in which it originates. Kölliker, however, quite correctly refers the formation of the several follicles to the continuous growth of connective-tissue septa between the cells of the epithelial cell clusters, to which he

has applied the term "gland-cords" ("egg-bands," or "chains," Frey).

Some, and sometimes very many, amongst the imbedded epithelial cells become conspicuous by their size and the size of their nuclei, as we have already seen to occur amongst the superficial epithelial cells, and where we may even still meet with them at this stage of development (see fig. 198). Pflüger (84, p. 113) has briefly noticed in his third provisional communication such very young egg cells in the ovarial epithelium of young cats, and has expressly termed them "evidently ova;" in his larger work, however, he has not any further followed this point. Other cells remain of small size, surrounding the larger egg cells as a kind of epithelium. It may easily be demonstrated further, by a comparison of younger with older ovaries, that the connective-tissue stroma between the imbedded masses of epithelial cells constantly undergoes increase, and especially grows in between the several egg cells with their epithelial investment. Thus each epithelial ball is divided by these ingrowing vascularized trabeculæ into as many cavities as it contains egg cells; but we occasionally meet at a later period with follicles containing two or more ova in their interior (see fig. 191). I need scarcely observe that the cells thus formed are the youngest or primordial follicles.

The shape of the cavities, within which the egg cells with their follicular epithelium are imbedded, varies considerably; rounded and oval forms alternating with long tubular formations (fig. 198), which last obviously become still longer as the interstitial tissue of the stroma augments; hence, in the human embryo of the 4—7 month we meet principally with spheroidal egg cavities, whilst in the newly born infant, and in children in the first years of life, elongated epithelial tubes are most common. The latter, or ovarial tubes are consequently secondary formations, which depend probably upon a certain free growth and development of the interstitial connective tissue, and are by no means necessary precursors of the Graafian follicles, as Pflüger (84), who attributes the greatest importance to them, maintains. This observer has described them as composed of a structureless membrana propria, by the inflections of which the several Graafian follicles are successively divided off. For myself, I have not hitherto been able to demonstrate the presence of such a membrane, and His

(52), Langhans (64), and Kölliker (59), have been equally unsuccessful. It is absent also, as we have remarked, in the follicles of Mammals; but, on the other hand, it is present at a later stage in the larger follicles of Birds (see fig. 194). During the dividing off of the follicles the egg cells remain for a time connected by means of their protoplasm, whilst the epithelial cells near the points of mutual attachment or poles of the follicle, after the complete separation of the latter, are characterized by their small size.

Fig. 198.

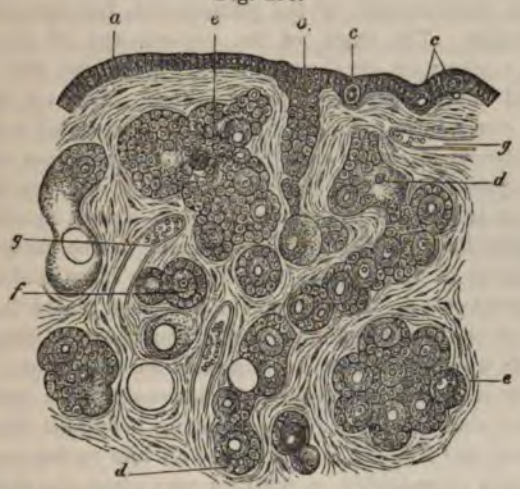

Fig. 198. Part of a vertical section of the ovary of a new-born Infant (Hartnack 3-7), with shut-up tube. *a*, Epithelium of the ovary; *b*, rudiment of an ovarial tube; *c c*, ova lying in epithelium; *d*, longer ovarial tube, with incipient formation of follicles; *e e*, egg balls, also with commencing follicular formation; *f*, youngest already completely isolated follicle; *g g*, vessels. In the tubes and egg balls the primordial eggs and the smaller epithelial cells, constituting at a later period the follicular epithelium, are to be distinguished.

According to the statements of Pflüger, the tubes lying close beneath the surface of the ovary terminate by cæcal extremities, and in these the germinal vesicles originate, surrounded by a diffuse protoplasm that forms a more definite investment for each as they become more deeply situated with the tube. Thereupon a number of these cells become conspicuous by their more vigorous growth, whilst the rest remain unaltered, and form the epithelial lining of the tubes.

The larger cells, which are the primordial eggs, occupy the axis of the tube. The eggs originating in this manner, which recalls that already given in regard to the Nematodes and Arthropods, are called by Pflüger pre-ova or primary eggs (Ureier). These subsequently increase in number by fission and germination, the products constituting the definitive eggs, that for a time remain connected with one another in the interior of the tubes in the form of a chain by processes of protoplasm, constituting the "egg chains" of Pflüger. The most important point in this now very generally accepted view, namely, the multiplication of the primary ova, has not come under my observation. The origin of the pre-ova and of the germinal vesicles in a tube with cæcal extremities, I must also, after what has been stated above, consider to be doubtful. Moreover, Pflüger, in one of his own figures (plate iii., fig. 1), has represented a connection existing between his tubes and the superficial columnar epithelium, and has frequently remarked that the contents of the egg tubes must proceed from the ovarial epithelium, which he always considers to be a serous epithelium; finally he returns again to the mode of origin just referred to of the eggs in cæcally ending tubes, and on this he lays very great stress. Bischoff and others have stated that the development of the ova terminates at the conclusion of fœtal life, an opinion with which my researches also lead me to coincide. Pflüger, on the other hand, has endeavoured to demonstrate the occurrence of a post-embryonal and periodically recurring neoplastic formation of ovarial tubes, and Kölliker is in accord with him on this point. The latter believes (*Gewebelehre*, p. 560) we may admit the formation of new follicles and ova to occur as a consequence of the growth of the epithelium of pre-existent follicles. I do not mean to deny that even in adults tubular and rounded groups of egg cells are present, the separate inclusion of which in follicles is not completed, especially as I have frequently seen similar formations in Dogs, Rabbits, and Birds, as well as inflections of the superficial epithelium (see fig. 192); still it remains an open question whether these are not the remains of earlier periods of development; at all events, I have not hitherto been able to satisfy myself that they are not so. The statements made by Koster (60) are to the same effect.

In reviewing the results of our inquiry it would appear, then, that the ova are not developed in and from the cellular elements of the vascularized ovarial stroma, as most observers prior to the suggestive work of Pflüger sought to demonstrate, but

that this stroma is only the support of a peculiar epithelial formation, which is developed from the very first as an independent embryonal structure, quite distinct from the stroma, and which in fact holds the same relations to it as the products of the two epithelial laminæ of the embryo do generally to their supporting and vascular connective tissue.

Pathological evidence, and in particular the development of numerous dermoid cysts in the ovaries, have long led observers to seek for cells belonging to the corneal lamina (hornblatte) in the substance of these organs. According to the well-known observations of His (52), however, it has not hitherto been possible to obtain any certain proof of this, from a consideration of the history of their development. Nevertheless, I desire to call attention to a work of Bambeke (6) that has very recently come under my notice, in which this observer states he has found in Pelobates fuscus that the most external germinal layer, from which the greatest part of the epidermoid structures are developed, on both sides of Ecker's yolk plug (Dotterpfropf), at the anal fissure of Rusconi and Remak, curls round in the interior of the ovum, and there forms a portion of the third germinal layer, whilst the remaining cells assume quite the characters of this incurved part. From this third germinal lamina both the internal genital organs and the Wolffian bodies are developed in the Batrachia; this observation may perhaps furnish a correct clue to the point in question. The reader is referred also to the similar statements made in the provisional communications of Götte (47a).

The early appearance of the ova is particularly worthy of notice; in all classes of animals they seem to be simply more highly developed epithelial cells of the ovary, that have undergone some peculiar modification, so that the follicular epithelium and the egg cells stand in a direct genetic relation to each other.

I take this opportunity of referring to the "polar cells" of El. Mecznikow (74). He found that in the Cecidomyidæ the earliest rudiment of the ovary, which was composed of a mass of cells, presented peculiarly formed cells, to which he applied the term "polar cells." These constitute the youngest ova.

If we may now regard it as certain that no new formation

of ova occurs at a later period, we have in these structures one of the most remarkable examples known of persistence of life in an elementary organism, lasting in Man for at least forty years.

The secondary growths of the primordial egg cells, forming the secondary yolk and the zona pellucida, have now been demonstrated to be the products of the follicular epithelium. Hence it is only the primordial egg that can be regarded as a simple cell, all mature ovarian ova being already compound structures.

This proposition is apparently in contradiction to the fact that the ova of Mammals and of Batrachia, as well as those of many lower animals, undergo fission with all their constituent parts. The contradiction, however, is not so complete and thorough as it appears to be. On the one hand it may be asked whether, in consequence of the genetic connection between the ova and the follicular epithelium, the products of the latter, when they are present in small quantities, cannot be completely assimilated to the original egg cells; on the other hand it is very doubtful whether, in the above-named classes, all the materials composing the ova can be applied directly to the construction of the embryonic body. At all events, Götte (47) has shown, in regard to the Batrachia, that the so-called "gland germ" of Remak, that is considered to be a product of fission, serves for the most part as aliment for the larva. Further and more exact researches in regard to the process of its fission and the behaviour of its products to the cells are still required.

There certainly appear to be eggs that possess no secondary yolk; for, independently of the ova of the Protozoa, respecting which no opinion can be formed at present, Ganin (41) has recently found in the section Pteromalina of the Hymenoptera mature ova in which there were no yolk granules, and the germinal vesicles of which were only surrounded by a small quantity of transparent protoplasm.

The resemblance of the ova of the several classes is obvious from the preceding observations. The primordial ova are everywhere identical; and the ripe ovarian ova of all Vertebrata are strictly comparable with each other, since they are all composed of the primordial ovum and other material proceeding after the same fashion from the follicular epithelium.

The various and in part very artificial classifications that have been sought to be established in ova are consequently resolved in a very simple manner.

It is more difficult to institute a comparison between the ovaries of different animals. In the lowest classes these appear to be reduced to their simplest yet most essential element, the egg cell, and we even find in many Vermes and Cœlenterata, in lieu of special organs, merely a few regions of the body wall coated with germinal epithelium, without any specially organized vascularized support, and the cells of this germinal epithelium increase without more ado into ova. Echinodermata Mollusca, and by far the greatest number of the Arthropoda, exhibit, on the other hand, special organs constructed upon the type of a tubular or acinous gland. And we further find in Mollusks and most Arthropods that arrangement of the Graafian follicles which is persistent in, and I might almost say which constitutes the characteristic feature of, the Vertebrata. In accordance with this the primordial ovum becomes enclosed by the growth of secondary structures in a peculiar cavity that is completely surrounded by a vascular stroma. The contrast appears to be worthy of notice that occurs in this respect between the higher Vertebrata and the lower, as the Batrachians and Osseous Fishes, and most of the Invertebrata. In the former a portion at least of the ovarial epithelium constantly remains freely exposed, whilst amongst the latter the whole of the epithelium is completely enclosed by the vascular stroma. We must conceive this enclosure amongst the Amphibia and Osseous Fishes so to occur that the germinal epithelium, which in all Vertebrata is expanded in a flattened manner, as well as the epithelium of the tube, becomes, as development proceeds, everywhere surrounded by a growth of vascularized stroma. In most Osseous Fishes this process is completed in immediate continuity with the Fallopian tube, the ovarium then appearing as the cæcal and expanded extremity of the latter. In the higher Vertebrata this total imbedding does not occur, being deficient at the ostium abdominale of the Fallopian tube.

The entire rudiment of the ovary is constructed precisely upon the type of the proper, *i.e.* of the epithelial, glands. We

find in it, as in them, rounded or elongated epithelial masses, imbedded in a stroma that serves as a support to vessels, and we may even consider the liquor folliculi and the secondary yolk to represent the secretion.

It remains to discuss the further history of the Graafian follicle, such as is seen in the process of ovulation, and in the formation of the *corpora lutea*. Both processes stand, as has long been imagined, but as has only recently been demonstrated by Spiegelberg (109), in the most intimate relation to each other.

Every ripe Graafian follicle presents at its most prominent part an elongated spot, free from bloodvessels and lymphatics —the hilum, stigma, or macula folliculi. At this point the wall of the follicle gives way during the exit of the egg. The circumstances giving rise to the rupture are of two kinds: on the one hand, as Spiegelberg has shown, an extensive fatty degeneration of the cells in the walls of the mature follicle occurs, and secondly, we have the development of the corpus luteum, which begins at a period long antecedent to the bursting of the follicle, and constitutes an impelling force. This substance consists of a considerable cell-growth, both from the sides of the follicular epithelium, and from the tunica propria folliculi; amongst the latter, numerous migrating cells occur, as I have ascertained from injections made with granular colouring matter. Coincidently with the migrating cells, vascular arcades project into the cavity of the follicle, in consequence of which this space becomes progressively diminished in size, and ultimately gives way at the non-vascular and weakest part of the wall. The ovum, and also in Mammals the liquor folliculi and the discus proligerus, the latter adherent to the ovum, are then set free. Whether there is in all instances a coincident discharge of blood appears to me to be very doubtful, and Pflüger (84) also denies its occurrence. That the menstrual congestion promotes rapid growth of the corpus luteum, and consequently exerts a direct influence upon the discharge of the ovum, is obvious from what has been already stated in regard to the mode of formation of the corpus luteum.

The corpus luteum first presents itself in a completely formed state a few weeks after the evacuation of the follicle; but

when impregnation has been effected, only after two or three months. It then appears as a mass occupying the previous position of the follicle, but exceeding it in size, and divisible into a central, usually red, but subsequently clear grey-coloured part, and an intensely yellow and plaited peripheral portion that is invested externally by what was formerly the tunica fibrosa of the follicle. In a recent corpus luteum the middle portion contains vascular connective tissue resembling mucous tissue, and numerous large cells filled with granular red colouring matter and crystals of hæmatoidin (see Zwicky, 129, and Virchow, 120). The peripheral zone is composed of two kinds of cellular elements; those that are situated most internally are large, polygonal, pale, and finely granulated cells that, as may easily be perceived in the Rabbit, proceed from the epithelium of the follicle; between these, vascular highly cellular processes everywhere extend, both from the periphery and from the centre, which give rise to the folding of the yellow zone. However abundantly the epithelial portion of the corpus luteum is developed in the first instance, it seems at a later period to disappear almost completely, a small residue of this voluminous structure alone remaining in the form of a white cicatrix—the corpus albicans. The cause of the retrogressive degeneration of the corpus luteum is referred by His (52) to an atrophy of the arteries, that are here provided with very thick walls. It is remarkable that with incipient pregnancy the corpora lutea, which are then distinguished as the corpora lutea vera, are developed to a much greater extent, and remain to the end of gestation, whilst the corpora lutea spuria disappear in the course of a few weeks. This seems to speak in favour of an additional purpose fulfilled by the corpora lutea, namely, to cover, as Pflüger (84) has pointed out, the loss of substance occasioned by the evacuation of the Graafian follicles.

We are indebted to His (52) for profound researches upon the corpora lutea. I am, however, unable to coincide with his view that the follicular epithelium does not participate in the formation of the corpus luteum, notwithstanding that it is entertained by Kölliker (59) and others; but must side with Schrön (102), Pflüger (84), and Luschka (72), who consider that both elements of the follicular wall contribute to its forma-

tion. Additional historical data upon the corpora lutea may be found in the dissertation of Zwicky (129).

Not all the Graafian follicles, the number of which is estimated by Henle in a young ovary at 36,000, and by Sappey (see Frey, 40, p. 534) at 400,000, attain maturity; and a few only furnish a ripe ovum. By far the greatest number die away at the most diverse periods of development; even the smallest follicles may be met with in a state of atrophy, as Pflüger has also observed (84). In the large atrophied follicles the remains of the ovum occur for the most part in the form of a very thick, highly refractile, compressed zona pellucida, with a small quantity of granular contents. The follicular wall undergoes alterations similar to those that occur in the formation of the corpus luteum, except that the neoplastic material is smaller in quantity. Well-formed corpora lutea occur only amongst Mammals; in the less developed condition, however, they are present in all Vertebrata, and large numbers of atrophied follicles may be discovered in all classes of Vertebrata.

Recent investigations made on Dogs have convinced me that the ovarial epithelium is deficient upon the surface of recently formed corpora lutea; on the other hand it penetrates very deeply between the ovarial stroma and the periphery of the corpus luteum at the point where the follicle has ruptured. Further observations are required to show whether or no a neoplastic formation of follicles and ova proceeds from these inflections of the epithelium.

PAROVARIUM (*Nebeneierstock*).—The Wolffian body consists, as J. Müller long ago demonstrated, and as Banks (7) and Dursy (35) have also shown, of two distinct structures; one consisting of a wide canal, with flattened granular epithelium, that is in connection with glomeruli. This constitutes the primordial renal part of the Wolffian body. The canaliculi of the second portion, that in Man includes the upper part of the Wolffian body, are narrower, and have a more columnar epithelium, which subsequently is in some parts ciliated. These, in the human subject, develop into the canaliculi of the head of the epididymis. In the female they penetrate to the hilus of the ovary, and in many species of animals, as in the Dog (fig. 191), the Cat, and the Cow, deeply into its stroma. They

here terminate by cæcal extremities, whilst after the obliteration of the Wolffian duct, from which they at an earlier period, in the greater number of animals, proceed, their lumen is shifted also from this side. The remains of these canaliculi, and consequently the remains of the sexual part of the Wolffian body, which is sometimes found situated externally to the ovary, constituting the *organ of Rosenmüller*, and sometimes within the ovary, as in the Dog, form conjointly the parovarium, which is the homologue of the epididymis of the male. In the human female it consists at a later period of from twelve to fifteen tubes imbedded in the ligamentum latum, which exhibit a fibrous and nucleated wall lined by a single layer of ciliated epithelium. The canals penetrating in the Dog deeply into the ovary are not ciliated internally, but are lined by pavement epithelium; they are clearly to be regarded as homologues of the tubuli seminiferi.

The remains of the pre-renal portion of the Wolffian body are also preserved in both sexes. In the male they represent the organ of Giraldès, the parepididymis of Henle (50), or the paradidymis (123); whilst in female embryoes they are sharply differentiated from the organ of Rosenmüller, and lie on the median side of this, between the ovary and the Fallopian tube, in the ligamentum latum. At a subsequent period an insignificant residue alone remains, which, however, may easily lead to the formation of many of the small cystic growths that are so common in the broad ligament.

A tolerably complete account of the older history and literature of the ovarium and ovulum is given by A. v. Haller (138), and by Valentin (139). The article by Farre, "Uterus and its Appendages," in Todd's Cyclopædia, Vol. v., and that by Leuckart, "Zeugung," in the "Handwörterbuch der Physiologie" of Wagner, may also be consulted. The more recent and important dates that may be mentioned are, that in 1827 v. Baer (2) discovered the ovum of the Mammal. The germinal vesicle had already been noticed in 1825 by Purkynê (88) in the egg of the Bird; and in 1834 Coste observed the germinal vesicle of the Mammalian ovum, which was quite coincidently discovered by Valentin and Bernhardt (13) in Breslau, and by Wharton Jones (140) in London. In 1835 R. Wagner (121, 122), with the demonstration of the germinal spot, provisionally brought the morphology of the ovum

to a conclusion. (See also 141, 142.) Wagner, in his Prodromus (121), instituted a comparison between the ova of all known classes of animals. He had already depicted the micropyle of the ovum of the Holothuriadæ in his Icones Zootomicæ. Doyère (143) appears to have already seen it in 1850 in Syngnathus. J. Müller (80) first described it minutely in the ovum of the Holothuriadæ, and compared it with the micropyle of plants. Keber (55) then expressly applied the term *micropyle* to this opening. We are indebted to Valentin in 1838 for the first demonstration of branched and tubular glandular structures in the ovary; an observation that was soon corroborated by Billroth (15), but to which little attention was paid until it was rediscovered by Pflüger (84), who in a detailed monograph led to the development of a different view respecting the structure of the ovary.

We have already given in the text, as far as space would permit, the views of Pflüger on the mode of origin of the Graafian follicles from tubes, on the development of the ova, their structure and their continuous new formation in adults, and the peculiarities of the ovarial epithelium. Formerly the follicles and ova were regarded as descendants of the ordinary stroma cells of the ovary; since Pflüger's time, however, both have been considered to be independent epithelial structures that are only imbedded in the stroma. It is nevertheless true that the demonstration of their first development still remains a desideratum.

Pflüger's investigations led to the publication of numerous works on the ovary. The tubular formations were soon also discovered in the human subject, first by Spiegelberg (107), and then by Letzerich (65), and Langhans (64); in the Fowl by Stricker (114) and many others, and very recently by Plihal (87) in Mammals. It must be confessed, however, that in opposition to Pflüger, who lays so much stress on the tubular structure of the ovary, stand the investigations of Borsenkow (22), Bischoff (19), Henle (50), Grohe (49), and the recent ones of His (52), who has paid especial attention to ovaries of embryoes, and first impressively pointed out their cavernous structure, with rounded and ovum-containing clusters of epithelial cells; also those of Kölliker (59). The work of Bornhaupt (21) must also be mentioned here, who first described in Fowls the development of the tubes of Pflüger from the epithelium of the ovary.

The statements made in the text upon the epithelium of the ovary, as well as upon the formation of the follicles and ova from it, may be compared with those given in No. 123 of the bibliography, with

which the observations coincidently undertaken by Koster (60) agree in all essential particulars.

In order to give a better general view I subjoin a small table with the measurements of the more important structures of the ovary above alluded to, according to the statements of Henle, Kölliker, Frey, and v. la Valette; they refer especially to the ovary of Man, and the numbers indicate micro-millimeters (thousandths of a millimeter).

Superficial epithelium of the ovary, newly born Child, length	15—18.
,, ,, ,, ,, ,, breadth	5—6.
,, ,, ,, of the adult . length	12—15.
,, ,, ,, ,, breadth	5—6.
,, ,, ,, of an old Cow length	9—12.
,, ,, ,, ,, Calf . ,,	12—15.
,, ,, ,, ,, Sow . ,,	15—20.
	Size of transverse section.
Primordial follicle, human embryo at the seventh month .	30—100.
Smallest follicle of the adult Woman	30—40.
Mature follicle ,, ,, . 10,000—12,000.	(10—12 mm.)
Smallest follicle of the Fowl	24—36.
Follicular epithelium (adult Woman)	15—22.
,, ,, of Fowl in follicles of 3—6 mm. in diameter	24—30.
,, ,, of Fowl in mature follicles . . .	6—8.
Primordial ovum of human embryo at third month . .	11—14.
,, ,, ,, at seventh month . .	15—25.
Smallest ova (adult Woman)	26.
Mature ovum of adult Woman	200.
,, ,, of Bitch	180.
,, ,, of Guinea-pig	120.
Zona pellucida of mature human ovum	10.
Germinal vesicle of human embryo at third month . .	9—11.
,, ,, ,, at seventh month . .	10—14.
,, ,, ,, of mature human ovum .	45.
Germinal spot of human embryo at third month . . .	2.
,, ,, of mature human ovum	7.
,, ,, of quite mature embryo of a Sheep . . .	5—8.
,, ,, of a Kitten seventeen days old. . . .	3—5.

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CHAPTER XXVI.

SKIN, HAIR, AND NAILS.

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PROFESSOR IN CRACOW.

A. Skin.

The skin (*integumentum commune*) constitutes an investment or covering to the entire surface of the body, and serves to protect it from external injury, though it performs many other and not less important purposes. In order to fulfil these objects, it is provided with various glandular, horny, and nervous structures that are not equably distributed over its whole extent, but are accumulated in particular regions. It thus becomes necessary to distinguish between the essential constituents of the skin, or those that are everywhere present, and those that are peculiar to special regions or districts.

To the former series belong the true skin, or corium, with its epidermic covering, and the subcutaneous connective tissue, or tela subcutanea; to the latter, the various horny structures, the hair and nails, the glands, and the terminal organs of the nerves, all of which require separate consideration.

The integumentum commune is composed of the cutis and the subcutaneous connective tissue, and the cutis again is subdivided into the dermis, or corium, and the epidermis. The dermis, or corium, is the most essential part of the skin, and forms a dense, but little elastic, white and opaque membrane composed of connective tissue. Its inner surface is continuous, without any sharp line of demarcation, with the subcutaneous

connective tissue, which also consists of connective tissue, but is distinguishable from the corium by its looser texture, greater succulency, and by usually containing much fat.

To the outer surface of the corium is applied the deepest layer of the epidermis, which here appears as a transparent, grey and soft, though superficially more dense, tissue. In consequence of putrefaction, maceration, or disease, the epidermis may become detached from the corium. The latter is attached to the more deeply seated structures, as the fasciæ and periosteum, by means of the subcutaneous connective tissue. This attachment is sometimes looser, sometimes closer, according to the texture of this tissue, and the amount of fat it contains. Over those portions of the body that exhibit much mobility the skin is loose, and the subcutaneous tissue is then free from fat, as in the eyelids and penis; or it is thrown into folds, as in the case of the extension surfaces of the joints.

The corium is not a plane surface in a physiological sense, but exhibits elevations of various sizes, with corresponding depressions; moreover folds and duplicatures occur, which, however, can be obliterated by traction of the surface, or by increased tension of the deeper portions; as, for example, as a consequence of exudation in the subcutaneous connective tissue, or from great increase in the deposit of fat. Smaller elevations are found upon the surface, in the form of lines, wrinkles, and papillæ. The former are especially well marked in the palm of the hand and in the sole of the foot, as well as on the palmar and plantar surfaces of the fingers and toes, where they form arcuate lines.

The smallest elevations are formed by the little warts or papillæ of the skin, which confer a felt-like appearance upon its free surface. The surface of the corium also exhibits numerous grooves and depressions, that either run between the folds and rib-like elevations, or pursue an independent course, as occurs opposite the surfaces of flexion of the joints of the extremities. These are best marked in those of the palmar surfaces of the hands and plantar of the foot. Lastly, we must mention the funnel-shaped depressions, called also the pores, of the skin, that are formed by the excretory ducts of the sweat and sebaceous ducts, and by the hair follicles.

Subcutaneous Connective Tissue.

The subcutaneous connective tissue is composed of fasciculi of connective tissue of various thickness, that, rising obliquely from the superficial fascia extend towards the under surface of the cutis. These fasciculi decussate with each other, and thus form a coarse meshwork, the spaces of which are subdivided by others of greater delicacy. The fasciculi are usually cylindrical, exhibit constrictions at various points like those of the arachnoid membrane, and consist of a number of sinuous fibres of connective tissue, between which lie numerous fusiform and connective-tissue corpuscles of various forms and dimensions. The subcutaneous connective tissue is in some places destitute of fat, as in the eyelids, penis, ears, and scrotum, and is only from 1 to 1·5 of a millimeter in thickness; elsewhere it contains in its meshes lobules of fat varying in size in different cases. When provided with fat, it forms the so-called panniculus adiposus. The fat lobules consist of a mass of sometimes oval, sometimes oblong, and by mutual pressure polyhedric fat cells, between which is a delicate plexus of blood capillaries. The fat cells themselves possess a very thin membrane enclosing a single drop of oily matter that is fluid during life, but otherwise usually appears in a coagulated state, and which keeps the cell wall so tightly stretched that it is rarely distinguishable during life. It can easily be exhibited, however, by extracting the fat with æther or with absolute alcohol and turpentine; a folded, very thin and transparent membrane then coming into view, in the interior of which a round nucleus is usually apparent. Remains of a granular substance (protoplasm), which is accumulated around the nucleus, may also be frequently found; occasionally, and especially in preparations preserved in spirit, the fat appears in the form of a pencil or sheaf of crystals.

In subcutaneous connective tissue destitute of fat, the above-mentioned secondary spaces are traversed by smaller fasciculi and in many cases even by individual fibrils of connective tissue, and in chromic acid preparations frequently present a triangular form, and are filled with a serous fluid.

The distance of the several fasciculi and fibrils from each other varies in different people, and under different circum-

stances, the variation depending on the succulency of the individual, and under pathological conditions, as, for example, in œdema of the skin, becoming very considerable. In the interior of the fasciculi of connective tissue, or in the spaces between them, fusiform cells lie scattered. In œdematous skin, where the cells and fibres run in an isolated manner through the œdematous fluid, it may be clearly seen that the connective-tissue cells consist of a granular mass of protoplasm, with two very long processes, that are usually given off from the opposite poles, but besides which are several that consist for some distance of granular material, though at a somewhat more distant point they assume the smooth appearance of a connective-tissue fibril. Such processes may be followed for a considerable distance into the fasciculi of connective tissue.

From this circumstance we may be permitted to draw the conclusion that in these cases, in accordance with the observations of Kusnetzoff on the skin of the embryo, the connective-tissue *cells* are continuous with connective-tissue *fibrils*.

In addition to the connective-tissue cells with long processes described above, we meet also with fusiform and round cells, resembling in their size and other characters the colourless corpuscles, as well as others that are larger, and possess a strongly granular protoplasm, in which a round or elliptical nucleus may, though perhaps indistinctly, be seen. The small round cells occur chiefly in the vicinity of the bloodvessels. On the other hand, we find numerous intermediate or transitional forms between the small round and the large cells that are provided with connective-tissue processes, and this not only in regard to the size of the cells, but also to the length of their processes.

At present we possess no precise information in reference to the development of the fat cells. Their relation to the blood corpuscles is worthy of notice. Nearly every fat cell is surrounded by a capillary bloodvessel, and to each fat lobule occupying a mesh of the subcutaneous connective tissue is distributed an arterial and a venous trunklet, between which a delicate capillary network is extended.

Through the subcutaneous connective tissue larger bloodvessels run to the corium, giving off branches to the fat lobules,

the hair follicles, and the terminal coils of the sweat glands. Nerves are also present that at certain points are provided with Pacinian corpuscles. Lastly, lymphatics here pursue their course independently of the bloodvessels. The larger lymphatics, that present a distinct circular muscular coat, possess special bloodvessels distributed to them alone, the vasa vasorum lymphaticorum; two such delicate bloodvessels, as a rule, accompany each lymphatic, and form by their frequent capillary anastomoses a close plexus around it. This explains the occurrence of the sharply defined red lines in the skin, which enable us to follow the course of the lymphatics in the subcutaneous connective tissue in cases of lymphangitis.

The Corium.

The corium is also composed of connective-tissue elements, between which runs a double network, consisting on the one hand of elastic fibres, and on the other of connective-tissue cells. The fasciculi of connective tissue traversing the subcutaneous tissue, and composed of a series of fibres, split, on reaching the deeper surface of the corium, into smaller fasciculi that extend in a somewhat oblique direction towards the surface, and constantly break up into finer and finer bundles. On reaching the corium, these fibres decussate with others which run at right angles both amongst themselves and to the former. A dense fibrous plexus, with very small meshes, is thus formed —meshes that, in specimens of dry skin, as well as in those that have been submitted to the action of tannic acid and of alcohol, are almost invisible, but are larger in the succulent skin of young persons, and attain their maximum in those pathological conditions that are accompanied by exsudation. In such specimens we may easily convince ourselves that the fibrils enclose rhomboidal spaces.

The regularity of this arrangement is disturbed at those points at which the skin is traversed either perpendicularly or obliquely to its surface by various structures, as hairs, sweat glands, excretory ducts, bloodvessels, and nerves, since these are accompanied by a sheath of connective tissue proper to themselves.

As already stated, the coarser fasciculi of connective tissue that penetrate the corium break up into more slender bundles, and these again into separate fibrils. In the deeper parts of the corium a few of the fasciculi decussate, and give a plexiform appearance to this part, whence it has been termed the *pars reticularis corii*, in opposition to the upper part, or *pars papillaris*, in which only a few of the fibres decussate. There is, however, no better defined line of demarcation between these parts than between the corium and the subcutaneous connective tissue in those cases where the latter is destitute of fat.

Fig. 199.

Fig. 199. Specimen prepared in chromic acid. *a*, Vascular, *b*, nervous papilla ; *c*, bloodvessel ; *d*, medullated nerve fibre, enclosed in a thick nucleated sheath ; *e*, tactile corpuscle ; *f*, transversely divided medullated nerve fibres.

The surface of the corium exhibits wart-like elevations, papillæ, that present differences in their height and breadth at different points, being sometimes villus-like or thread-shaped processes of the cutis, as on the fingers, and sometimes more rounded projections, as on the greater part of the rest of the

body. In consequence of the presence of these papillæ on the skin, the arrangement of the fibres undergoes some modifications. In particular, the fibres running parallel to the surface penetrate the papillæ, and are at the same time drawn out into long loops. The course of these most superficial fibres is, however, not quite straight, but gently sinuous, so that neither the surface of the corium nor that of the papillæ is quite plane.

The vertical fibres of the corium also extend into the papillæ, accompanying the bloodvessels in their centre, and probably terminating by free extremities.

The surface of the corium is everywhere invested by a thin membrane, that is most distinctly brought into view in specimens prepared with chloride of gold. In these we find that intermediate to the red or blue-coloured mucous layer and the similarly coloured corium is a thin, transparent, and uncoloured layer, in which, here and there, oval nuclei are imbedded, lying parallel to the surface of the corium. The line of demarcation between this membrane and the corium is not well defined, but it is much more sharply expressed towards the mucous layer, which, independently of slight furrows, is in many cases finely toothed. Seen from the surface it exhibits fine ribs or even prickles, which project amongst the cells of the mucous layer. According to Czerny, after treatment with solution of nitrate of silver, it presents a few areas like those seen in the walls of the lymphatics. Elastic fibres constitute an essential constituent of the corium, forming in the deeper parts a coarse-meshed, but nearer the surface a closer plexus, and after the clearing up of the connective tissue by means of acetic acid, become conspicuous by their sharp outlines and spiral course.

In addition to the elastic and connective-tissue fibres, cells are found, which are either distributed as fusiform cells through the fasciculi of connective tissue, or form stellate and anastomosing cells, lying between the fasciculi in the deeper parts of the corium, or between the individual fibres of the more superficial parts. Fusiform cells also lie between the connective-tissue fibres ensheathing the larger bloodvessels and capillaries. Moreover we find round or oval cells, resembling the colourless corpuscles of the blood in form and size, lying for the most part

immediately adjacent to the bloodvessels, though often also at a considerable distance from them. The number and size of the cells vary in different individuals, and appear to stand in relation to the succulency of the skin. In young persons their number and size are equal to those of the cornea, the forms of which, after treatment with solution of chloride of gold, are similarly liable to variation.

The *papillæ* of the skin are divided into the vascular and the nervous papillæ. Medullated nerve fibres are always present in the latter, passing to the bodies called tactile corpuscles by Meissner. The former only contain vascular loops.

The size and number of the papillæ vary considerably in different parts of the skin. They are most developed on the palmar surface of the hand and fingers, where they form obtuse cones with circular bases, and are arranged in a double series along the above-mentioned striæ. Their length in this part amounts to 0·1—0·2 of a millimeter, and they are either almost in contact at their bases, or are separated by only a small distance, whilst in other regions they scarcely attain half this height, and only form slight elevations of the surface. They often coalesce at their bases, and then form compound papillæ. The thickness of the whole dermis is not less variable. It not only presents differences in thickness in various parts of the skin, but it varies also in different individuals of one and the same race. According to Krause, the thickness of the dermis, which, on account of the gradual transition of the corium into the subcutaneous connective tissue, can only be approximatively estimated, amounts in the eyelid and prepuce to 0·56 of a millimeter; on the glans penis, to 0·27 of a millimeter; upon the face, on the penis, and on the area around the nipple, to 0·76—1·12; on the forehead, to 1·52; on most other parts of the body, to 1·69—2·25; and on the back, the sole of the foot, and palm of the hand, to 2·25—2·28 of a millimeter.

Bloodvessels of the Corium.

The vascular trunks passing obliquely upwards through the subcutaneous connective tissue to the corium, after having first given off branches to the fat lobules, the ducts of the sudo-

riparous glands, etc., form in its deeper parts a close vascular plexus, from which again oblique branches are given off to the more superficial portion. Near the surface of the corium, and between its pars reticularis and papillaris, is a second vascular plexus, the meshes of which are finer than the former, and indeed correspond in their size to that of the bases of the papillæ. Simple capillary loops, proceeding from this plexus, penetrate the papillæ, and running near their axes reach almost to their extremities. It is not every papilla, however, that is provided with a vascular loop; since, speaking generally, those papillæ into which medullated nerve fibres enter are destitute of vessels, although there are numerous exceptions to this rule.

Lymphatics of the Skin.

It is necessary, in the case of the skin, to distinguish between lymphatic vessels and lymphatic spaces. The former constitute closed tubes, bounded by proper walls, whilst the latter are lacunæ between the bloodvessels and lymphatics that are filled with lymph. The lymphatics of the subcutaneous connective tissue provided with a muscular coat anastomose frequently, and run obliquely to the deep surface of the corium, where, like the bloodvessels, they form a double plexus, one lying upon the other (Teichmann, Young).

The lymphatic plexus of the upper part of the corium lies beneath the vascular plexus, and forms polygonal meshes of small vessels, that, according to Teichmann, have a diameter of 0·018 to 0·054 of a millimeter. The deeper plexus lies again beneath the deeper vascular plexus, and consists of larger vessels with coarser meshes than the upper. The anastomoses between the two plexuses are effected by a few relatively large vessels running obliquely from one to the other. In the natural state no lymphatics enter the papillæ; but in the hypertrophied papillæ of the sole of the foot a few branches penetrate to about half their length, and terminate cæcally (Teichmann).

The walls of the lymphatics in the upper part of the corium present cell markings that can be brought into view by means of nitrate of silver, subjacent to which, in the deeper-seated lymphatics, is a fine plexus of elastic fibres.

In the description of the corium and of the subcutaneous connective tissue we have spoken of spaces that occur between the fibres, and are filled with serous fluid, varying in quantity with the succulency of the individual. In pathological conditions, and both in acute and chronic exsudations, as in œdema, these spaces are essentially the seat of the effused material.

Such spaces occupying the interspaces of the fibres of the corium have no proper walls; as is shown by the fact that the œdematous fluid of a wide area will discharge itself through a comparatively slight cut in the skin. These spaces are designated lymph spaces, although no direct communication between them and the lymphatics has been demonstrated.

The relation of the bloodvessels to the lymphatics is worthy of special notice. Although the course and ramifications of the larger lymphatics are independent of the bloodvessels, appearances are frequently presented, especially in œdematous skin, which tell in favour of the existence of some specific relation between the two sets of vessels. Thus each lymphatic is accompanied for considerable distances by a capillary bloodvessel, and not unfrequently by two, which lie in immediate contact with it, or may even be imbedded in its wall to nearly half their depth. According to Langer, in the skin of the Frog two lymphatics accompany the larger bloodvessels. In the subcutaneous tissue of Man these relations are so far different, that in many parts, as in the penis and the extremities, the larger lymphatics are accompanied by two bloodvessels, by the capillaries of which they are surrounded.

By various writers, as by Stricker, perivascular lymphatics have been described, whilst their existence has been denied by others (Langer). In the human skin the bloodvessels are certainly not invested by lymphatics possessing a proper wall lined by epithelium. We have stated above, however, that the bloodvessels, and even the capillaries, are enclosed by parallel fibres of connective tissue, and fusiform connective-tissue corpuscles. Between these and the vascular wall we find, as elsewhere, spaces containing serum, the width of which varies, and which may be quite correctly termed perivascular lymphatic spaces.

Epidermis.

Vertical sections of the skin show that the corium is covered externally by a layer of cells distinguished as epidermis in its wider sense, and, according to Malpighi, capable of division into two superimposed layers, an external, the proper *epidermis*, and an internal, the mucous layer, *stratum mucosum—Rete vel Mucus Malpighii*. The latter is composed of epithelial cells, that fill up nearly all the depressions of the surface of the corium, and consequently exhibit on their inferior surface eminences or pits corresponding to the elevations or depressions of that surface; the former, on the other hand, is composed of epidermal scales, that, arranged in lamellæ, give to the section a lamellar or fibrillated appearance.

Mucous Layer.

The first series of cells composing the mucous layer do not exceed 0·006 of a millimeter in diameter, are provided with an oval nucleus, and are usually columnar in form, with their long axes directed perpendicularly to the surface of the corium. They consist of a slightly granular refractile mass of protoplasm, destitute of cell membrane, surrounding, though in small quantity only, the compact nucleus. In many instances, as, for example, in newly born children, the limits of these cells so completely disappear that the surface of the corium appears to be covered by a homogeneous layer of protoplasm, with regularly distributed nuclei (Henle). The series of cells immediately superimposed upon this layer are cubical. These are of larger size, possess a better-defined outline, and an oval feebly granular nucleus, in which two nucleoli are often visible. Their surface usually exhibits flat ribs or teeth. The cells of the next three rows successively increase in size, assume a polygonal form, and contain one, or occasionally two or three, round nuclei. They are homogeneous in structure, with a distinct membrane, which in most parts of the skin gives off small hairlike processes or prickles which penetrate the immediately adjoining cells. (Rib or prickle cells of Max Schultze). The nearer we approach the surface of the mucous layer, the more

flattened is the form assumed by the cells, so that they come to lie with their long axes parallel to the surface of the skin. The cell bodies become more rigid and more homogeneous, the nuclei smaller, and often surrounded by a bright halo. In preparations hardened in chromic acid, they easily fall out of the section, leaving a spherical cavity; but we may still more frequently meet, in the cells of this series, with round empty spaces corresponding in size with the cell nuclei, to one side of which a crescentic crumpled and flattened nucleus is attached. There are small vacuolæ within the cells, that especially occur in the most superficial cells of this layer, and in the fresh state are probably filled with a clear fluid.

Besides the cells that have just been described, presenting the general characters of epithelial cells, others of a different nature are here and there found in the mucous layers when obtained from the living subject. These are most easily distinguished in the middle and upper layers of the cells forming the mucous layer, where they can be recognized by the refraction of their protoplasm, and by their minute size. They are commonly elongated, appearing as if they had been compressed between two epithelial cells, or they give off fine processes that run between the several epithelial cells. Their protoplasm is highly refractile, and becomes deeply stained by carmine, whilst the nucleus can only be recognized with difficulty. This is usually distinguishable, however, after being subjected to the imbibition of carmine. In the deepest cell-rows of the mucous layer such cells are much more difficult to demonstrate, since they offer some points of similarity to the cells of which these are composed; for the cells of these layers possess a similar highly refractile protoplasm, become deeply stained with carmine, and only differ from the former by their well-defined nucleus. They are most easily perceived in those cases in which one half is found between the cells of the mucous layer, whilst the other half is imbedded in the corium (Biesiadecki). These cells strongly remind one of the so-called migrating cells. They are met with in the subcutaneous connective tissue, where they are for the most part found in the neighbourhood of the bloodvessels, and also between the fibrillæ of the corium; and we find them again in the

mucous layer, where in the normal state they are only sparingly present, though they become very numerous in pathological conditions (pointed condylomata, eczema, Biesiadecki).

Portions of skin that have been hardened in chromic acid or Müller's fluid are best adapted for the investigation of the mucous membranes, and are at all events superior to those that have been prepared in alcohol. The above-described vagrant or migrating cells are only extremely rarely found in portions of skin that have been removed from the dead body. They are much more abundant in the young, and in those portions of their skin that have a thick mucous layer. They are most readily seen in irritated portions of skin, as after the application of a blister, or in the part covering diseased bone, and finally in œdematous skin.

The fact that we find these cells sometimes half buried in the corium, sometimes presenting all possible forms in the different layers of the rete mucosum, that they augment in numbers in irritated portions of skin, and that they are only sparingly present in the healthy state, are all points in favour of their locomotive power, especially as in other structures provided with cells possessing similar characters their change of position can be followed.

The epithelial cells of the mucous layer are separable from each other with difficulty either by mechanical or chemical agents: and their intimate union is due, not so much to the presence of any cementing substance, but to the interlocking of these prickles and ribs. The isolation of the cells of this layer is most easily accomplished in fragments of skin that have been hardened in chromic acid, and then boiled for a considerable period in moderately concentrated solution of potash. The mucous layer then becomes entirely detached from the corium, and the epidermis cells then readily fall asunder by gently tapping them with a glass rod.

The Superficial or Horny Layer of the Epidermis.

The horny layer, or stratum corneum (*Hornschichte*), appears on section as if composed of slightly sinuous fibres running

parallel to the surface of the skin. Even with high magnifying powers, but little further insight into the structure of this layer can be obtained. Such insight can only be gained by isolating the apparent fibres, and it is then seen that they are composed of a number of flat polygonal scales, the so-called epidermal scales, or horny laminæ.

In the deepest tier, lying in contact with the mucous layer, the cells are rather thicker than those more superficially placed, and resemble the uppermost cells of the mucous layer, but are somewhat flatter than these, less granular, and do not become stained with carmine. In most cases the nuclei have entirely disappeared, but occasionally a flattened slightly oval nucleus is visible, having an average diameter of 0·005 to 0·008 of a millimeter. The scales of the upper tiers are flatter, of various form, crumpled, with a sharply defined simple outline, nucleated and transparent. In water they swell up to some extent, become opaque, darker, and more granular; in acetic acid or caustic potash they become vesicular, with fine fibres or granules in their interior, or with a folded structure in the centre resembling a nucleus. The lamination of the epidermis, that gives it the appearance of a fibrous structure on section, arises from the firm adhesion to one another of the scales of each tier. The stratum Malpighii does not completely fill up all the inequalities of the surface of the corium, but presents minute elevations at the points corresponding to the projections, or papillæ, of the latter; and between these elevations are slight depressions. The lamellated epidermis follows these elevations and depressions of the mucous layer, which explains the wavy course of each lamella on section. The whole epidermis, however, follows the deeper furrows of the corium, as, for example, the ribs and furrows of the palm, forming the well-known markings of the cutaneous surface.

The thickness of the epidermis varies considerably in different individuals and in different parts of the body. It often forms a very thin membrane lying on a thick mucous layer, whilst in many cases it is twice or three times as thick as the latter. In both regions, however, the mucous layer maintains a uniform thickness, with the exception only of those parts of

the skin that possess long papillæ, *between* which the mucous layer exhibits a remarkable thickness, whilst it is relatively very thin *over* them.

The thickness of the mucous layer, according to Krause, is from 1-65th to 1-20th of a line; on the other hand the epidermis varies from 1-65th to 1 line.

The two together frequently measure 3·7 millimeters, but the usual thickness is from 0·05 to 0·25 of a millimeter.

The dark colour of the skin that in some individuals is general, but in others appears only in certain parts of the body, as in the area around the nipple, the scrotum, etc., depends on the presence of pigment in the cells of the mucous layer. In the coloured parts the lowermost cells of the rete mucosum contain fine granular brownish-yellow pigment corpuscles in proportions varying with the depth of the cutaneous tint. In the cells lying immediately above these are a few pigment granules giving an uniform light-yellow colour to the protoplasm, the colour diminishing in intensity in the uppermost cells of this layer and in the scales of the epidermis, so that the discoloration of these latter can only be perceived by direct comparison with perfectly colourless cells. The black colour of the skin in the negro depends also upon the pigment contained in the cells of the mucous layer. In pathological formations as in conical condylomata (Biesiadecki), the above-described vagrant or migrating cells also contain pigment corpuscles.

Nerves of the Skin.

Up to a late period medullated fibres with their peculiar terminations, the corpuscles of Pacini and Meissner, were alone known to exist in the skin. More recent researches have demonstrated, in addition, the presence of an abundant non-medullated nervous plexus ending by free extremities between the cells of the mucous layer.

The subcutaneous nerve trunks divide at the inferior surface of the corium into several branches that accompany the larger bloodvessels, and are composed of both medullated and non-medullated nerve fibres. The nerves of those parts of the skin in which the tactile and Pacinian corpuscles are especially

numerous, contain a larger portion of the medullated nerve fibres.*

From the primary branches a few medullated nerve fibres are given off either in the subcutaneous connective tissue, or in the lowermost portion of the corium, which terminate in the Pacinian corpuscles.

The remainder of the fibres extend for the most part in an oblique direction towards the surface of the corium, and form a nerve plexus in the stratum papillare corii that accompanies the blood vascular plexus.

A few medullated nerve fibres often lose their medulla even in the upper part of the corium, or they may extend into the nerve papillæ, and terminate in the tactile corpuscles.

The non-medullated nerve fibres accompany the bloodvessels of the vascular papillæ (Langerhans).

Pacinian Corpuscles.

These corpuscles were first seen by A. Vater, as Langer has demonstrated, and have hence been also called the corpuscles of Vater. They are present, not only in Man, but in many Vertebrates and Birds, and are for the most part seated in the subcutaneous connective tissue, though they may be found in some other parts, as, for example, in the mesentery (in the Cat). In reality they are nothing but the remarkably thickened ends of medullated nerve fibres.

The sheath consists at first of a homogeneous nucleated membrane, on which, by immersion in a solution of nitrate of silver, indications of the presence of an epithelium can be made to appear. At a certain point it breaks up into a system of twenty or thirty concentric capsules, resembling the coats of an onion, that constitute the principal mass of the corpuscle. Of these membranes, which are clear and apparently structureless, the external are thicker, and separated from one another by a clear fluid, whilst the internal are thinner, and are in very close apposition. On section, especially after the action of acetic acid, numerous oblong nuclei come into view, that

* Langerhans. Virchow's *Archiv*, Band xliv., 2 and 3 Heft.

assume a red colour with chloride of gold. When seen from the surface, the membranes, both when fresh and after treatment with various reagents, exhibit a slightly punctated, homogeneous appearance, with only indistinct indications of striation.

Solution of silver brings out markings resembling those on the lymphatics.* These consist for the most part of irregularly pentagonal areas, bounded by sinuous dark-brown lines, within which the above-mentioned nuclei lie.

The medullated nerve fibres enter these terminal onion-like structures in a spiral manner, and extend into the cavity of the innermost and smallest capsule. The axis-cylinder runs up the middle to its blind end, and there ceases with one or several finely granular terminal bulbs.

The nerve medulla, on the other hand, fills this cavity, forming either a finely granular mass (the internal bulb of Kölliker) or an irregularly and coarsely coagulated body, that appears dull in comparison with the nerve medulla, but, like it, assumes an intense violet-black colour when treated with solution of chloride of gold.

In close proximity to the nerve fibre a large bloodvessel penetrates into the interior of the corpuscle, and forms a close capillary plexus between the outer capsules.

In Man the corpuscles of Vater measure from 1·1 to 4·5 millimeters in length, and are constantly present on the cutaneous nerves of the fingers and toes, on those of the palm of the hand and sole of the foot, and on the articular nerves of the extremities (Raeuber). They are comparatively rare on other cutaneous nerves, and are only occasionally found on the great sympathetic plexus near the abdominal aorta, behind the peritoneum, and near the coccygeal gland.

The Corpuscles of Meissner or Wagner—Tactile Corpuscles.

The medullated nerve fibres that, like "creeping roots," pursue a tortuous course beneath the cutaneous papillæ, in com-

* Hoyer. Reichert und Dubois' *Archiv*, 1864, 1865.

pany with the bloodvessels, here and there penetrate particular papillæ that, as a rule, are destitute of vessels, and terminate in the so-called tactile corpuscles (Corpuscula tactûs) of Meissner and Wagner.

If the skin covering the last phalanges be subjected to examination after being hardened in chromic acid, scattered broad and but slightly elevated papillæ will be met with, containing oval corpuscles that equal the papillæ in length, and have a diameter of 0·02 to 0·045 of a millimeter. These (fig. 190) are conspicuous for their rigid aspect and their transverse striation, which is partly owing to the presence of fine lines, and partly to fusiform transversely placed and highly refractile nuclei. A medullated nerve fibre enclosed in a sheath, containing many nuclei, runs sometimes to the lower pole, sometimes as far as the middle, and sometimes even to the extremity of the corpuscle, frequently winding once or more times round the corpuscle which is constricted at these points. The nerve at length suddenly loses its medulla, and is no longer capable of being traced.

Similar appearances are presented by fresh sections of skin treated with potash, soda, or concentrated acetic acid. Many points, however, yet remain undecided in regard to them, and receive different explanations at the hands of different observers. Thus the transverse lines are considered by some to be caused by connective-tissue fibres; others regard them as elastic fibres, and others as nerves; whilst the transverse nuclei are sometimes held to be connective-tissue corpuscles, and sometimes the nuclei of nerve sheaths. The nerve sheaths now become destitute of medullary substance, are again by a few observers considered to enter a cavity within the tactile corpuscle, and to end by free extremities after the fashion of the corpuscles of Krause, that are elsewhere found.

Specimens that have been prepared with chloride of gold, enable us to give an explanation of some of the appearances in question, since in these the nerve fibres assume a dark violet colour, whilst the rest of the tissue becomes of a pale red. The contours of the corpuscles are marked out by faint outlines into areas within which are oblong nuclei. In fine sections of the corpuscles, from four to six violet-coloured

nerve fibres can be distinguished running sometimes obliquely, sometimes longitudinally, which are accompanied by less deeply tinted small nuclei; such sections, however, furnish no information in regard to their ultimate course or division.

The corpuscles of Meissner are thus, like those of Pacini, the terminal structure of a medullated nerve; but we are still unacquainted with the mode of termination of the axis-cylinder.

The tactile corpuscles are most constant and most numerous in the terminal phalanges of the fingers. According to Meissner,* there are on each of these 108 tactile and 400 vascular papillæ. They occur in smaller numbers on the palm of the hand and sole of the foot, and on the dorsum of the hand and foot, whilst they are not constantly present on the nipple (Kölliker, Krause), nor on the lips (Kölliker, Krause, Henle).

Termination of the non-medullated Nerve Fibres.

The non-medullated fibres form, by the side of the vascular plexus of the pars reticularis corii, a plexus composed of a few thick and many very fine smooth and varicose nerve fibres, by the side of which are numerous nuclei. A few fibres pass off from this plexus towards the mucous layer, beneath which they sometimes run for some distance, and then suddenly bend to enter its substance. Others extend to the papillæ, in which they divide, and ascend between the cells of the mucous layer (Langerhans, Biesiadecki). These relations can only be seen in specimens stained with chloride of gold; but the preparation of the skin by this method is a matter of great difficulty, on account of the thorough imbibition of the corium being generally only incompletely effected, in consequence of the impermeability of the epidermal layers. For this reason Langerhans has recommended that a few drops of acetic acid should be added to the solution of chloride of gold, in which the thin sections of the cutis are macerated.

In specimens thus prepared the nerve fibres that enter the mucous layer are rendered visible, and terminate with bulbous extremities at about the level of the third tier of cells. Langer-

* *Beiträge zur Anatomie und Physiologie der Haut.* Leipzig, 1863.

hans has also seen in the higher layers of the rete a considerable number of dark-violet bodies, from each of which a single process is directed downwards, whilst several run towards the stratum corneum. The former he believes to be continuous with the more deeply seated nerve-fibres.

Sebaceous Follicles.

The sebaceous follicles (*glandulæ sebiferæ*), also named on account of their connection with the hairs, glands of the hair follicles, are simple or compound acinous glands, the excretory duct of which rarely opens immediately upon the surface, but, as a rule, into the hair follicle. In the case of the larger hairs they appear to be appendages of the follicle, whilst in pubescent hairs the relation is reversed, the small hair follicles appearing to open into the wide excretory duct of the gland. They are always situated in the corium, and never reach into the subcutaneous connective tissue.

The sebaceous follicles consist of gland substance and an excretory duct. The former is composed of gland lobules (Acini) or sacculi, of pyriform shape, filled with enchymatous cells, of which from two to twenty open into each excretory duct. The gland lobules thus consist of a gland sac (sheath) and enchyma cells.

The gland sac is composed of a transparent and colourless nucleated membrane that is apparently destitute of structure, but when treated with solution of silver exhibits groups of cells; externally it is bounded by a dense layer of connective tissue, with elastic fibres, which is traversed by a moderately close vascular plexus. The sebaceous follicles are not known to possess any special supply of either lymphatics or nerves.

The enchyma cells that fill up the whole of the interior of the saccule, with the exception of a small central cavity, consist of epithelial cells, of which the most external, that lie in contact with the gland sac, resemble the deeper cells of the mucous layer, except only that the nucleus is more distinctly visible. Those that are situated more internally first become filled with small fat molecules, and then with larger fat drops that surround and conceal the nucleus, and cause the cells to increase in size. After the fat has been extracted, round spaces

of various size remain in the sharply defined polygonal cells, corresponding to the position of the fat drops which are enclosed by the rest of the protoplasm. The round vesicular nucleus occupies the centre of the cell.

In many cases the peripheric gland cells are also filled with fat, whilst in other cases the quantity of fat they contain is very small. The cavity of the sebaceous glands is occupied by an amorphous mass of fatty matter, and the *débris* of numerous cells.

The wall of the excretory duct is continuous with the gland sac on the one hand, and with the hair follicle on the other; so that the gland sac may be regarded as a protrusion of the hair follicle, and this more especially, because the root-sheaths circumscribe the excretory duct of the gland, and are directly continuous with its enchyma cells.

The wall of the excretory duct consists of a transparent membrane, with an epithelial investment, enclosing a cylindrical canal which is for the most part filled with fat. The cells correspond in every particular with those of the external root-sheath of the hair follicle, and are covered by an epidermal layer that diminishes in thickness towards the gland.

The number and size of the glands are by no means proportionate to the size of the hair. Those connected with the larger hairs consist of several lobules that surround the middle third of the hair follicle like a crescent, and are only separated from it by a small quantity of connective tissue. The size of the glands depends, on the one hand, on the number of lobules, and on the other, on the number of the enchyma cells, and the quantity of fat they contain.

The excretory ducts of the sebaceous glands, of which there are one or two, open into each hair follicle at an acute angle, so that ultimately the cells are continuous with those of the external root-sheath (Henle).

The gland lobules of the pubescent hairs are in some parts larger and more numerous than those of other hairs, and their excretory ducts are then also surpassingly large.

The sebaceous glands are entirely absent in the palm of the hand and sole of the foot, as also on the dorsum of the third phalanges and on the glans penis.

The development of the sebaceous glands commences at the third month in Man, by the formation of a projection of the cells forming the external root-sheath at the level of the future gland. These epithelial cells subsequently increase in number, and then appear as a pyriform process of the root-sheath.

Sweat Glands.

Sweat glands (*glandulæ sudoriparæ*) are tubular glands contorted into a knot, and opening on the surface by a straight excretory duct. In each sweat gland, therefore, we must distinguish between the gland knot and the excretory duct.

The gland knot (fig. 191) forms a small, roundish, yellow body, which almost always lies in the subcutaneous connective tissue, but is occasionally found in the lowermost parts of the corium. Its diameter is usually from 0·15 to 0·5 of a millimeter. Those of the axilla measure from one to two millimeters, and a few even as much as five millimeters.

In the glomerulus the tubular duct of the gland is much contorted, and held together by loose connective tissue. The blind end of the tube lies in the centre of the knot, and is somewhat enlarged, measuring in one case three-fourths of a line (Krause).

The gland tube is composed of a sheath, lined by enchyma cells. The sheath is a delicate transparent membrane, that, when acted upon by nitrate of silver, exhibits areas in which are oblong nuclei (Czerny).

The loose connective tissue between the windings of the tube is composed of fine fibres that run parallel to it, and contains scattered fusiform connective-tissue corpuscles. It forms a kind of capsule around the gland knot, and is traversed by a narrow-meshed vascular plexus.

In the larger glands, as in those of the axilla, numerous longitudinal muscle cells lie on the outside of this membrane, giving a striated appearance to the surface of the gland.

The gland tube is lined by a single layer of conical or columnar cells.

Inasmuch as the gland knot lies in the subcutaneous connective tissue, the excretory duct of the sweat gland must

necessarily perforate the entire thickness of the corium as well as the mucous and epidermal layers. It either runs straight or with only a slightly sinuous course through the corium, and always enters the thick mucous layer *between* the papillæ, traversing this in a spiral manner.

Fig. 200.

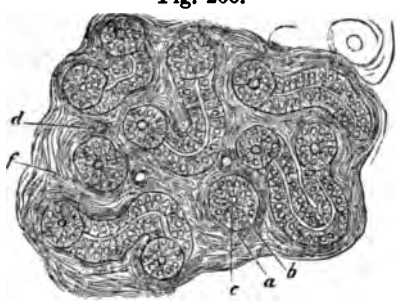

Fig. 200. Glomeruli of Sudoriparous gland, divided in various directions. *a*, Sheath of the gland; *b*, enchyma cells; *c*, gland tube; *d*, divided bloodvessel; *f*, loose connective tissue, forming a capsule to the gland.

As the cubic cells of the rete mucosum become converted into the flat scales of the epidermis, the excretory duct must present a greater number of coils in proportion to the thickness of the latter; where the epidermis is thin, the tube scarcely forms a semispiral; where it is thick, however, there may be as many as twenty, which on both sides of the body turn in corkscrew fashion to the right (Welcker). In a few regions, as on the hands and feet, the external opening is funnel-shaped and is visible even to the unaided eye as the sweat pores. In these parts the apertures are situated at regular distances from each other in the furrows between the striæ, but elsewhere they usually open in groups (Krause). None are found upon the prepuce or glans penis.

From the level of the rete mucosum, outwards, the excretory duct has no special wall, but is bounded in the rete mucosum itself by concentrically arranged concavo-convex cells, and in the epidermis by the scales of which it is composed.

In the corium the duct is formed by a tap-shaped process

of the rete mucosum, which, in skin that has been macerated for some time, can be withdrawn, in company with the epidermis, as a fine fibre (Eichhorn's fibre). It here possesses a special wall, that is to be regarded as a prolongation of the membrane investing the corium.

The rete mucosum is continued down the tube as a layer composed of many tiers of cells, that progressively diminish in thickness, till in the lower part of the corium they ultimately pass into the enchyma cells. The duct in its passage through the corium is accompanied by numerous connective-tissue fibres and connective-tissue corpuscles running parallel to it, and usually also by two small bloodvessels.

Langerhans (*loc. cit.*) describes structures situated between the cells lining the upper part of the duct, belonging to the nervous system, similar to those found in the mucous layer.

According to the estimates of Krause, there are 2,736 sweat glands in every square inch of the palm of the hand; 2,685 on the sole of the foot; 1,490 on the dorsum of the hand; 1,303 on the neck and forehead; 417 on the back and buttock. The sweat glands of the axilla cannot be directly compared, as regards their number, with those of other parts of the body, on account of their remarkable size.

The development of the sweat glands commences at about the fifth month of pregnancy with the formation of a flask-like process of the rete mucosum, that dips into the corium, terminates in a swollen bulbous manner, and is composed of epithelial cells. At the seventh month the gland assumes an elongated tubular form, the blind end being bent and widened like a retort. During the last months of pregnancy this end becomes contorted, and forms the glomerulus of the gland.

Muscular Tissue of the Skin.

Striated or voluntary muscular fibres only reach the skin from the deeper-lying parts in the face, the beard, and nose, ascending sometimes obliquely, sometimes vertically, between the hairs and the sebaceous follicles, to terminate in the corium.

Smooth muscular fibres are arranged in two different

methods in the skin. On the one hand they run horizontally, and form either an anastomosing plexus (Kölliker), as in the scrotum (*Tunica dartos*) and prepuce, or circular fasciculi, as in the area of the nipple and in the nipple itself.

On the other hand they traverse the corium obliquely in the form of single fasciculi, with a diameter of 0·045—0·22 of a millimeter, and are in immediate relation with the hair follicles (constituting the muscles of the hair follicles of Kölliker, or *Erectores pili* of Eylandt). They arise in the upper part of the corium, and run obliquely in immediate proximity to the sebaceous glands, to the hair follicle, into the inner sheath of which they are inserted just below the sebaceous gland. Many hairs possess two muscles, that decussate over the sebaceous gland, and encircle it crescentically. As the hairs are inserted obliquely in the skin, forming a moderately acute angle with the surface, whilst the muscular fasciculus lies in the plane of the corresponding obtuse angle, the contraction of the latter must obviously cause the hair to become more erect (goose-skin).

Neumann describes oblique muscular fasciculi as existing in the skin that have no connection with the hairs.

B. Hairs—Pili.

Hairs are cylindrical horny structures, inserted into tubular depressions of the skin—the hair follicles, from a papilla at the bottom of which—the hair papilla—their development proceeds.

In describing the hair we must therefore consider—(1) The structure of the *hair follicle* and *hair papilla;* and (2) the *hair;* and in the latter again the part including the papilla, or *hair-root*, and the part projecting beyond the skin, or *hair-shaft.*

Hair Follicle.—The *hair follicle* is a depression of the surface of the corium, that exhibits a blind inferior extremity (fig. 201 *c*), the so-called dilatation of the hair follicle and a free funnel-shaped and dilated excretory duct (*a*).

Below the excretory duct the hair follicle is contracted,

and forms the so-called neck. The excretory duct of the sebaceous follicle opens at this point.

Proceeding from the neck of the hair follicle towards its dilated extremity, we distinguish (*a*) the *hair sac* or *follicle*, and (*b*) the *root-sheath*.

The hair sac consists of three layers, the external, the middle, and the internal.

The *external sheath of the hair follicle* (*d*) (external fibrous membrane of Kölliker) consists of compactly arranged fibres of connective tissue running parallel to the axis of the hair, and intimately united above to the fibres of the corium, whilst inferiorly they surround the dilatation of the hair follicle, and accompany for some distance the bloodvessels distributed to the papilla. Externally this sheath, losing its defined contour, passes gradually into the connective tissue of the corium, whilst it appears to form an independent sheath, having a thickness of 0·02 of a millimeter, to that part only of the hair follicle that is imbedded in the panniculus adiposus.

Within this sheath are two longitudinal bloodvessels (a small artery and vein), that with their transverse anastomoses form a trellis-work surrounding the hair follicle, together with here and there a dichotomously dividing medullated nerve fibre.

The middle layer of the hair follicle is the *internal sheath of the follicle* (*c*), the internal fibrous membrane of Kölliker. It is composed of a few transverse fibres of connective tissue, between which is a homogeneous, slightly granular material, containing numerous rod-shaped, transversely arranged nuclei. After treatment with nitrate of silver, oblong areas bounded by sinuous lines may be distinguished at numerous points (Czerny). The nature of these areas has not yet been satisfactorily determined. They resemble smooth muscular fibres in their fusiform shape and rod-like nucleus, whilst the circumstances that they can only be isolated with difficulty, and that they swell up in water without becoming cloudy, speak in favour of their being of the nature of connective tissue (Henle, Kölliker).

The strong contraction of this sheath that occurs, for example, when the hair falls out, demonstrates its muscular nature (fig. 196).

Numerous capillaries proceeding from the bloodvessels distributed to the external sheath of the follicle penetrate the

Fig. 201.

Fig. 201. Hair of the beard. *b*, Neck of the hair follicle ; *a*, excretory duct ; *c*, dilatation of the hair follicle ; *d*, external sheath of the hair follicle ; *m*, fat cells ; *e*, internal sheath of the hair follicle ; *p*, papilla ; *f*, external root-sheath ; *g*, internal root-sheath ; *h*, cortical substance ; *k*, medullary substance of the hair shaft ; *l*, root of the hair ; *n*, arrector pili ; *t*, sebaceous gland ; *o*, papillæ of the skin ; *s*, mucous layer (rete mucosum) ; *ep*, epidermis, which is continued into the excretory duct of the hair follicle.

internal sheath, and form a close plexus in its substance. No nerves have hitherto been found in it. It first makes its appearance at the level of the neck of the follicle, and in the stronger hairs of the beard forms a layer surrounding their lower part, of the thickness of 0·05 of a millimeter. It surrounds also the bulb, and is continuous at its base with the papilla (*p*) which projects into the cavity of the follicle, and is usually seated, by means of a peduncle, upon the internal sheath of the follicle.

The *papilla of the hair* exhibits a thin neck and a thicker body with a conical extremity. On the average its length is twice as great as its breadth. Its thickness, and not its length, stands in relation to the length of the hair (Schrön).

The papilla consists of fibrous connective tissue, the fibres of which proceed from the internal sheath of the follicle, and are intermingled with numerous round nuclei, together with well-defined round nucleated cells. Its surface is perfectly smooth, and at the neck it is surrounded by the vitreous membrane of the hair follicle, though this cannot be demonstrated to extend over the bulb.

Two small arteries enter the papilla. These usually unite to form a single trunk towards the summit and then again divide to form two emergent vessels (veins). Numerous anastomoses occur between these four vessels.

I have been able to follow non-medullated nerve fibres as far as to the neck of the papilla.

The third and innermost layer of the hair follicle is composed of a transparent membrane—*Vitreous membrane*—having a thickness of 0·005—0·008 of a millimeter, and remaining unchanged both in acids and alkalies. Notwithstanding that this layer appears perfectly homogeneous on section, it exhibits, when viewed on the flat surface, transverse, obliquely decussating, delicate fibres, and here and there also ill-defined round nuclei.

Diluted solution of silver brings markings into view on the vitreous membrane that resemble those of the walls of the lymphatics (Czerny).*

The outer surface of this membrane, which is in contact

* *Centralblatt für die med. Wissenschaften*, 1869, No. 26.

with the internal sheath of the follicle, is smooth; whilst its inner surface exhibits delicate transverse ribs or prickles, resembling those of the prickle cells (Haight).*

The vitreous layer is a continuation of the basement membrane covering the surface of the corium; it lines the internal sheath of the hair follicle, extending as far as the neck of the papilla, and becoming gradually thinner before it ceases. It would appear, however, that, reduced to an extremely thin lamina, it covers the body and even the apex of the papilla.

Neither bloodvessels nor nerves are to be found in the vitreous layer.

The *root-sheaths* (*f*) that we have already alluded to as additional constituents of the hair follicle, consist of two layers, the outer and the inner root-sheaths.

The *external root-sheath* (*f*), is formed by the rete mucosom that is continued into the hair follicle from the surface of the skin, but does not extend as far as the bulb, terminating usually at the level of the apex of the papilla, or in many cases even above it (Moleschott, Chapuis). It consists of several layers of epithelial cells, of which those in contact with the vitreous membrane are usually columnar, and exhibit a nucleus situated in that part which is most distant from this membrane.

The cells succeeding to this internally are polyhedral, whilst the innermost are flattened, and include an oval nucleus.

In the neck of the hair follicle the external root-sheath is thinner than elsewhere, chiefly in consequence of the several layers of cells of which it is composed presenting a more flattened form. Towards the hair bulb the layer terminates generally in a rounded manner, presenting a triple tier of cells, but sometimes more pointedly by becoming reduced to only a single row of flat cells. In specimens prepared with chloride of gold, fine varicose dark-violet fibres may be found here and there between the cells of the external root-sheath, which proceed from the vitreous membrane, and extend as far as to the inner root-sheath. The probability that these are nerve fibres has not up to the present time been supported by any proof that they are continuous with the nerve fibres distributed to

* *Sitzungsberichte der Akademie in Wien*, 1868, Band lvii.

the sheaths of the hair follicles. Langerhans (*loc. cit.*) describes nerve cells between the cells of the external root-sheath similar to those of the rete mucosum.

The *internal root-sheath* (*g*) is composed of two layers, an outer and an inner. The outer layer is the inner root-sheath of Henle; the inner, the so-called sheath of Huxley. In regard to their development, their composition, and their chemical characters, these two structures are perfectly distinct. The first is genetically connected with the external root-sheath, whilst the latter is developed with the hair itself from the bulb.

The *internal root-sheath of Henle* appears in longitudinal sections of the hair as a thin, transparent, and refractile layer, scarcely staining with carminate of ammonia, and closely resembling the vitreous membrane. It begins at the neck of the hair follicle, and only extends towards the bulb as far as the external root-sheath. Externally it is sharply defined from the external root-sheath, whilst internally it is in contact with the sheath of Huxley, that will be subsequently described.

The first-named sheath, originally described by Henle, by whom it was named the inner root-sheath, consists, as is shown by sections and surface views, of oblong, non-nucleated, highly refractile scales, running parallel to the long axis of the hair follicle, and resembling vertically-divided fusiform cells. The plane surfaces of these spindle-shaped cells are applied to the external root-sheath, over which they form a continuous layer, whilst their internal convex surfaces touch the cells forming Huxley's sheath.

The greater number of anatomists have described small fissures between these scales, and the presence of these has led Henle to describe it as a fenestrated membrane; on the other hand they have been regarded as small holes produced by the manipulation requisite for the isolation of the sheath.

There can be no doubt that, in surface views, without previous isolation of the sheath, appearances are seen that speak in favour of the presence of fine fissures between the scales. These apparent fissures, however, are produced by the focussing of the internal surface of the cells, that, as already stated, are convex, whereby sometimes broader, sometimes narrower slits appear, according as the cells brought

into the focus are more superficially or more deeply situated. We may easily satisfy ourselves, by means of transverse sections, and with appropriate focussing, that the scales are in immediate contact with one another by the borders of their plane surfaces.

In the lower parts of the hair follicle, the internal root-sheath consists simply of a single row of the above-described scales, that are easily to be distinguished from the cells of Huxley's sheath, which are here still nucleated. At a higher point the former become more flattened, whilst the latter lose their nuclei, so that the two sheaths can no longer be sharply distinguished from each other. It nevertheless appears that the scales of the internal root-sheath increase in number above. Lastly, it may be observed that the scales of the internal root-sheath swell up and then dissolve in solutions of potash and soda.

HAIR.—The *hair* itself is composed of a larger part that projects beyond the surface of the skin, the *hair shaft*, and of a bulbous enlargement of the shaft, the *hair root*, from which a proper sheath that surrounds the lowermost part of the hair, and constitutes the so-called sheath of Huxley, together with the cuticula of the root-sheath, are developed.

If we examine a transverse section of a hair shaft to which no reagents have been previously applied, it will be seen that the margin is finely toothed, whilst the surface of the shaft is crossed by fine lines, enclosing rhomboidal spaces, which correspond to the apices of the teeth. The appearances presented remind one involuntarily of the surface of the body of the scaly Amphibia, and are the expression of thin scales investing the hair, and representing the *cuticula* of the hair first described by Hermann Meyer.

The chief mass of the hair is formed by the *hair substance* (fig. 201, *h*), *i.e.*, a substance that in grey hairs is colourless, lustrous as silver, and in which numerous fusiform longitudinal dark-coloured granules occur. In coloured hairs, the hair substance, which is also called the *cortical substance*, includes a variable quantity of differently coloured pigment granules.

In the thick hairs of the beard, and also occasionally in the hairs of the head, a *central medulla* occupies the interior of

the cortical substance (fig. 201, *k*), and is composed of granular polyhedric cells; it can be most distinctly seen in grey hairs.

The shaft of hairs that have not been cut terminates in a fine and always non-medullated point, and in the other direction passes gradually into the root.

The *root of the hair* (fig. 192, *l*) is that part of the hair that surrounds the papilla, and occupies the deepest part of the hair follicle. The bulbous portion is composed of nucleated cells resembling those of the lowermost tiers of the rete mucosum, and differing from them in all probability only in possessing a certain degree of solidity.

The cells lying next to the papilla are columnar, and arranged vertically upon its surface, in many instances being attached only by a delicate thread. The outermost cells are in contact with the vitreous membrane of the hair follicle, and are somewhat flattened, whilst those forming the middle portion of the root are polyhedric, and contain a large and well-defined nucleus.

In the middle of this mass of cells a series may be perceived at the level of the papillary body, running parallel to the vitreous membrane, and distinguished from the rest by being more closely arranged, by being flattened from above downwards, and by becoming intensely stained with carmine.

At the level of the apex of the papilla, or even in many instances somewhat lower, a series of small scales, arranged perpendicularly to the axis of the hair, appear as a continuation of this row of cells, but above the papilla they become more and more parallel to the axis of the hair, so that the lower cover a great part of the upper ones, leaving only about a sixth part of the upper surface free. As these scales become progressively more and more closely applied to each other and fuse together, they form the cuticle that is recognizable as a clear and finely toothed border surrounding the hair.

These cuticular cells occurring in the middle of the hair root divide it into a central portion surrounding the papilla, and a peripheric part, that is in contact with the vitreous membrane, and is scarcely one-fourth of the thickness of the former.

The middle part of the root of the hair consists, as we have said, of columnar cells resting upon the papilla, and more

externally of polyhedric cells superimposed upon these. These cells are characterized by their large round nuclei, that stain deeply with carmine, and by the sparing quantity of homogeneous protoplasm of which they are composed. Above the papilla the amount of the protoplasm augments. Both the cells and the nuclei are at first oblong, but at a higher level become fusiform with rod-shaped nuclei.

In this part, which usually exceeds the length of the papilla, the hair root gradually diminishes in thickness, and is still bounded by the obliquely-placed scales of the cuticle. The cells composing the root here also become stained with carmine.

The outlines of the individual cells cease to be visible at a tolerably defined limit, fine lines appearing in their place, that seem to be formed by fibrillated and elongated nuclei. The whole mass no longer stains with carmine, and forms in grey hairs, from which this description is taken, the stiff, silvery, and horny cortical substance of the hair shaft. *Thus the axile portion of the hair root enclosed by the cuticle cells is continuous with the substance of the hair, whilst the cells that in the first instance are spheroidal—the so-called hair cells—become continuously more fusiform, and ultimately converted into thin horny and spindle-shaped bodies.*

The peripheric portion of the hair root lying between the cuticle cells and the vitreous layer of the hair follicle is continuous with the cuticle of the root-sheaths and with the sheath of Huxley.

Its deeper-seated part consists of at least three layers of cells, of which the most external are elongated in the direction of the long axis of the hair, whilst those applied to the cuticle are for the most part polygonal.

The cells adjoining the cuticle of the hair introduce themselves between the scales of which it consists, and become converted into the scales that form the cuticle of the root. These scales overlap each other like those of the hair cuticle, with this difference, that the upper cover the greater part of those lying more deeply, or, in other words, the free uncovered borders of the scales of the hair cuticle look upwards; those of the cuticle of the root-sheath, on the other hand, downwards.

These two layers of cuticle are firmly attached to each other; for, on tearing out a growing hair, both, as a rule come away, together with the inner root-sheath of the hair, and it is only in rare instances that the hair alone is pulled out with the inferiorly covered scales of the hair cuticle.

At the level of the papilla the external cells of the peripheric portion of the hair root become elongated in the direction of the long axis of the hair into fusiform cells, the lower ones becoming filled with a few, the upper with numerous, highly refractile granules, that usually conceal the shrunken nucleus.

In the lower part of the hair follicle these cells are in contact with the vitreous membrane; and higher up, with the internal root-sheath of Henle, already described, which is composed of fusiform, but non-nucleated, epidermic cells.

The former, or deeper cells, are distinguished from the latter by the circumstance that a nucleus is still visible in their interior, and that they are filled with highly refractile granules, which become only feebly tinted with carmine, whilst the others are destitute of nuclei, and do not stain with carmine at all.

The most external cells of the hair root constitute a special sheath to the hair, which, having been first described by Huxley, is termed the sheath of Huxley. At the level at which the hair is still composed of distinct nucleated and soft cells, that easily stain with carmine, this sheath consists of nucleated fusiform cells, filled with small refractile granules; but above this level the cells are destitute of nuclei, and form a sheath that, in consequence of the fusion of the contained granules, appears homogeneous in longitudinal section, and similar to the vitreous layer, and coalesces with the internal root-sheath of Henle to form the single internal root-sheath of authors.

This internal root-sheath formed by the coalescence of the inner root-sheath of Henle with Huxley's sheath, reaches as far as to the neck of the hair follicle, where, according to the statements of most anatomists, it terminates by undergoing fibrillation. Well-prepared longitudinal sections, however, show that the internal root-sheath, becoming considerably attenuated, is continued along the neck of the hair follicle. Its scales become suddenly flattened at the beginning of the neck of the

hair follicle into epidermic scales that, arranged in several layers, cover the external root-sheath, which is also composed of flattened cells. In many cases, however, it occurs that this sheath constitutes an investing membrane to the hair throughout the neck of the hair follicle and the excretory passage; though in most cases its composite scales coalesce with the epidermic scales of this passage.

The topographical arrangement of the different sheaths can only be thoroughly investigated in successful longitudinal sections. Thick and grey hairs are best adapted for examination, since they can be easily divided longitudinally, and because the want of pigment permits the various cells of the hair substance to be distinctly seen. Preparations made with needles and transverse sections then complete the picture.

As the papillæ of the hair are situated at different depths, no two present the same appearances, although the section may have been carried quite parallel to the surface. The appearances vary in fact with the height at which the hair has been divided. Sometimes a papilla composed of connective tissue will be seen invested by several layers of epithelium-like cells, that are again enclosed by the vitreous membrane; this is a transverse section of the neck of the papilla. It is bounded by the cells of the hair root, in which neither the cuticle nor the sheath of Huxley can be differentiated. The external root-sheath is as yet absent.

In other instances, again, the medulla of the hair, composed of oblong quadrangular cells, may be seen to occupy the axis of the cortex, which consists of nucleated polyhedric cells. The cortex is bounded by several concentrically arranged fine lines, between which are delicate oblong nuclei (cuticle of the hair and of the root). External to these is a layer composed of a double row of cells, which contain, not only many bright granules, but also distinct nuclei (Huxley's sheath), enclosed by a single series of highly refractile, hemispherical, non-nucleated cells, that do not stain with carmine (internal root-sheath of Henle), forming a layer that is again invested by the epithelial cells in contact with the vitreous membrane (external root-sheath).

The section here has been carried through the still soft root

of the hair, at a point above the papilla that does not exceed the length of the papilla itself.

At still another plane (fig. 202) the transverse section of the hair exhibits the substance of the hair, composed of a rigid, horny, homogeneous material, in which small round nuclei appear (*e*, the transverse sections of the nuclei of the hair cells). The periphery is more transparent, and is indistinctly striated (*h*, cuticle of the hair). This is invested by a single series of

Fig. 202.

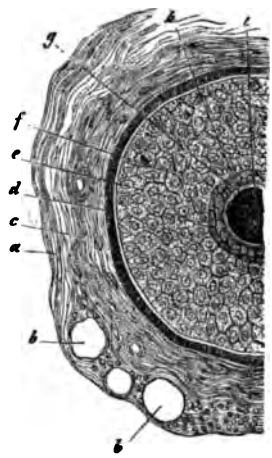

Fig. 202. Section of a hair below the level of the neck of the hair follicle. *a*, External sheath of the hair follicle, with transversely divided bloodvessels *b* ; *c*, internal sheath of the hair follicle ; *d*, vitreous layer of the hair follicle ; *e*, external root-sheath ; *f*, scales of the internal root-sheath of Henle ; *g*, sheath of Huxley ; *h*, cuticula ; *l*, hair.

bright rigid cells, that include shrivelled nuclei (*g*, Huxley's sheath). Outside these are the nucleated cells (*f*) of the internal root-sheath of Henle, and the epithelial cells of the external root-sheath (*e*). Here the section has struck the shaft of the hair at about the end of the middle third of the hair follicle.

In other sections of the hair the cells of Huxley's sheath are destitute of nuclei (as in fig. 195), and can no longer be distinguished from the cells of the internal root-sheath, so that a

double or triple series of non-nucleated cells surround the shaft of the hair.

At the level of the neck of the hair follicle the hair shaft is invested by four or five rows of epidermic cells. In the excretory passage of the hair follicle, which may contain two hairs, each hair is surrounded by multiple layers of epidermal cells (modified sheath of Huxley, together with the internal root-sheath of Henle), that are again included by epidermic layers (constituting the horny layer of the excretory passage).

Transverse and longitudinal sections show also (1) that the horny substance of the hair is developed from the hair cells —that is to say, from the cells of the root surrounding the papilla; (2) that the cuticle of the hair is also formed from the cells of the hair root; (3) that the cuticle of the root-sheaths and Huxley's sheath develop from the peripheric cells of the hair root. And lastly, (4) that the internal root-sheath of Henle corresponds to the horny layer of the external root-sheath.

The development of the constituents of the hair shows also that the sheath of Huxley, in opposition to the views of Kölliker, must grow like the hair itself; that the hair is not thrust upwards within the cuticle of the root-sheath, but between Huxley's sheath and the internal root-sheath of Henle; and that the latter, corresponding to the constantly advancing horny layer of the external root-sheath is likewise thrust outwards through the neck of the hair follicle.

The forces by which these movements are effected are— (1) The constant production of new cells on the papilla at the root of the hair, and (2) the pressure that the internal sheath of the follicle, tightly embracing the root-sheaths, exercises in forcing the contents of the follicle through the excretory passage.

The cells forming the deeper parts of the hair root resemble those of the rete mucosum in their chemical characters. Acetic acid renders the protoplasm more transparent, and the nucleus more distinct. Dilute solutions of potash and soda cause them to swell up, and then quickly dissolve both the cell and the nucleus.

In the description of the influence of reagents upon the hair

it is requisite, according to Moleschott,* to take into consideration, not only their strength, but the temperature at which they are applied, and the duration of their action.

In concentrated sulphuric acid the cuticle of the hair swells to an extraordinary degree, forming a sheath to the hair substance that may even exceed the thickness of the hair itself. When warmed to 40°—50° C. (104°—122° Fahr.), the cuticle breaks up in a few hours into separate scales.

It disintegrates more slowly in solutions of potash containing 4·6 per cent., or in those of soda containing 3 per cent. In the course of forty hours the cortex of the hair appears spiny, owing to the elevation of the cells forming the cuticle that are still adherent by their lower borders.

The cortical substance of the hair, which can be split longitudinally by mechanical means, breaks up, under the action of concentrated sulphuric acid, into separate scales or laminæ (fibre cells), having a length of 0·05—0·08 of a millimeter, and a breadth of 0·004—0·01 of a millimeter, and containing thread-like nuclei with a length of 0·02—0·03 of a millimeter.

The medullary cells can be rendered very distinct by macerating hairs for a few days in a two per cent. solution of potash. If the solution be stronger, they dissolve, and on the addition of an excess of acetic acid to the solution, white precipitates are thrown down, that give Millon's and Fourcroy's reaction.

Very strong solutions of potash dissolve and destroy the hair; in solutions of potash containing 4·6 per cent. the sheath of Huxley breaks up into its constituent cells, without swelling up like the hair cuticle.

The hair follicles vary in their length with the length and thickness of the hair. Those of the long hairs of the head, and thick ones of the beard, extend into the subcutaneous connective tissue; those of the larger hairs on the surface of the body, as far as the lower part of the corium; whilst the papillæ of the finest hairs (lanugo) are situated in the upper part of the corium. They do not, however, run vertically, but always form an acute angle with the surface of the corium.

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* *Untersuchungen zur Naturlehre*, Band iv., Heft 12.

However variable the length and thickness of the hairs may be the above-described constituents are always present.

The different colours presented by the hair depend chiefly on the pigment contained in the hair cells, that either exists in the form of granules, or is equably diffused. But the colour of the hair also depends on small bubbles of air that either occur between the cortical scales and the medullary cells, or are found in their interior. Langerhans maintains that the papillæ are surrounded by a considerable number of double-contoured nerve fibres. In specimens prepared with chloride of gold it may be demonstrated that varicose fibres belonging to the non-medullated nerve fibres which accompany the bloodvessels into the papilla, extend from the bulb between the cells of the hair root, and run parallel to the papilla to its apex.

Development and Succession of the Hair.

The first rudiment of the hair follicle and of the external root-sheath, in the human embryo, occurs at the end of the third or the beginning of the fourth month as a club-shaped depression of the surface of the corium, into which the cells of the mucous layer are prolonged, and which they completely occupy.

A finger-shaped column is thus formed from cells of the rete mucosum, which is as yet destitute of a special investing membrane, being only surrounded by the connective-tissue fibres of the corium.

A further rudiment of the hair is formed at the bottom of this process as a short column half its thickness, and, like it, composed of cells.

Between these cells, that may be distinguished from those of the before-mentioned process by their large nuclei and small amount of surrounding protoplasm, bloodvessels soon make their appearance, and the smaller column is then recognizable as the rudiment of the hair papilla, which in lanuginous hairs is characterized by the abundance of its cells.

Around the papilla that has thus been formed small round cells soon accumulate, causing the hair follicle to deepen, and making a cavity for themselves in the column formed by the

mucous layer. As these cells become converted into long spindles, they penetrate further and further into the column of the mucous layer, pressing it outwards in all directions, so that the cells of which it is composed come to constitute the cells of the external root-sheath.

The cells surrounding the papilla form the root of the hair, and from them both the hair itself and the sheath of Huxley are developed. Those in immediate proximity to the papilla remain soft, but at the point where they are already contained in the external root-sheath they soon become horny. This has led several observers to maintain that the apex of the hair is first formed, and that the root is developed subsequently; on the contrary, others have adopted the view that the axial cells of the column formed by the mucous layer become converted into the cells of the hair proper.

The peripheric cells of the root of the hair become the scales of Huxley's sheath, which also invests the apex of the hair. Both remain for some time within the external root-sheath, bounded above by the cells of the mucous layer, but gradually both the latter and the epidermis, as well as the external sheath, are perforated by the growing hair, and the point of the hair enclosed by Huxley's sheath comes into view. Finally, the hair appears to grow more rapidly than the sheath of Huxley, which at length it also penetrates.

The development of the hair follicle has not been accurately studied.

The first rudiments of the hair do not make their appearance simultaneously in all parts of the body; and it would also appear that the time required for their development up to the period of eruption, is different in different parts of the body. The first to appear are those of the eyebrow and eyelashes, then those of the head, and subsequently those of the rest of the body. Nearly all the hairs project beyond the surface of the body at the twenty-fourth week.

Hairs of embryoes developed in this manner are always lanuginous; *i.e.*, are very minute, with short hair follicles. In many regions the lanuginous hairs are permanent; but in others thick hairs are subsequently developed, by which they are replaced.

Where a thick, permanent hair, the papilla of which extends as far as the subcutaneous connective tissue, replaces a fine lanuginous hair, the papilla of which only reaches to the middle layer of the corium, it is obvious that the hair follicle of the lanuginous hair must become elongated.

This occurs, as Kölliker has described, by the external root-sheath sending off a process into the deeper layers of the corium. In the same mode, as in the formation of the first rudiment of the hair, a papilla develops at the base of the epithelial column from the hair follicle, the cells of the root accumulating around it. The hair and Huxley's sheath proceed from the cells of the hair root, and perforate the cells of the epithelial process, and then, lying in immediate contact with the lanuginous hair, penetrate into its follicle.

The papilla of the lanuginous hair now appears to undergo atrophy, the hair falling out, and the thick persistent hair then occupying its follicle. This process of succession of hairs is not, in all probability, limited to a single occurrence during the first year of life, but is frequently repeated in childhood, as the skin augments in thickness.

The permanent hair increases to a certain length, differing with the individual and the region of the body. When it has reached its proper limits, the papilla can no longer support the weight of the hair, which falls out, a new hair developing at the same spot. This is the physiological succession of hair, which in Man is continuous, but in animals occurs periodically.

The fall of the hair results from the circumstance that no new cells form around the papilla. The last-formed cells of the hair root, receiving no impetus from behind, become converted into hair substance, and form either the conical or club-shaped inferior extremity of the hair shaft, which is composed of fibrillated hair scales.

In accordance with the statements of Henle, most anatomists have described the club-shaped end of a shed hair as a second form of hair root (hair bulb of Henle), though incorrectly, since these bulbs are only the ends of hair shafts that have ceased to grow.

The sheaths of the hair follicle, that in consequence of their muscular structure (?) exert a constant pressure upon the con-

tents of the hair follicle, force the clubbed extremity of the hair, together with the sheath of Huxley, continuously upwards, and so contract that the vitreous membrane presses directly on the papilla; whilst at a higher point the internal surfaces of the external root-sheath come into contact (fig. 203)

Fig. 203.

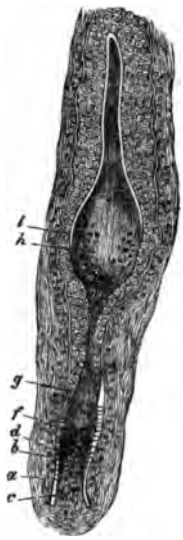

Fig. 203. Shed hair, after typhus fever. *a*, External; *b*, internal sheath of the hair follicle; *c*, hair papilla; *d*, vitreous membrane; *g*, external root-sheath; *h*, club-shaped end of the hair, connected by a cord with the papilla, *f*; *l*, external root-sheath terminating on the clubbed extremity of the hair.

The new hair is developed from the old papilla.* Hairs shed in consequence of disease are either not succeeded by new hair, or in their place lanuginous hairs are formed.

c. Nails—Ungues.

The nails are horny, elastic, transparent, concavo-convex laminæ, that lie imbedded in folds of the skin on the last phalanges, and cover the greater part of their dorsal surface.

* Langer, *Denkschriften der K. K. Akad.*, 1850 (fig. 191).

We must hence, in considering the nails, regard (1) the nail itself; (2) the portion of the skin covered by the nail or bed of the nail; and (3) the wall of skin that includes three sides of the nail or groove for the nail.

The nail itself presents an anterior free border, a posterior and two lateral borders that lie in the groove for the nail; a convex upper surface, that for the greatest portion of its extent is free, and an inferior surface attached to the bed of the nail.

The posterior part which is imbedded in the groove is the root of the nail, and the rest constitutes the body.

The surface of the skin covered by the nail, or nail bed, is divisible into a posterior part, or matrix unguis, covered by the root of the nail; and an anterior part, the proper bed of the nail. The skin bounding the posterior and lateral borders of the nail forms a wall, the nail wall, that is thickest posteriorly, becomes thinner anteriorly, and forms with the nail bed the so-called nail fold or groove (Nagelfalz).

The nail bed passes anteriorly into the skin of the ball of the finger, and posteriorly and laterally into the inferior surface of the nail wall, which is turned towards the nail. It consists of subcutaneous connective tissue, corium, and rete mucosum.

The subcutaneous connective tissue of the nail bed is characterized by the absence of fat, and by the course of the ascending connective-tissue fibres which arise as separate fasciculi from the periosteum of the last phalanges, expand above in a brush-like manner, and are directed somewhat backwards towards the root of the nail. Between the several fasciculi are spaces filled with loose connective tissue, or frequently by a few fat cells, and they also enclose numerous vascular loops.

The course of the fasciculi of connective tissue in the corium of the bed of the nail resembles that of other parts of the skin, except in the unusual number of the fibres ascending from the subcutaneous cellular tissue, which are elsewhere rare as compared with the horizontal bundles.

The nature of the surface of the corium of the bed of the nail constitutes, however, its most characteristic feature, though its posterior part, which we have termed matrix unguis, presents some differences from the anterior part, or proper nail bed. The surface of the matrix of the nail, which lies on a somewhat

lower plane than the nail bed, is covered with papillæ directed forward (Henle), and implanted on low mound-like elevations of the corium. The height of the papillæ varies from 0·1 to 0·2 of a millimeter, and their breadth from 0·03 to 0·06 of a millimeter. At an arched line parallel with the tip of the finger, and usually covered by the nail wall, the surface of the proper nail bed is covered with from fifty to ninety ribs, having a height of from 0·1 to 0·2 of a millimeter. These ribs, which are prolongations of the mound-like elevations of the matrix, increase in height towards the free border of the nail, and are continuous below the free edge with papillæ, having a diameter of as much even as 0·5 of a millimeter. The ridges are chiefly composed of vertical and parallel fibres of connective tissue, between which numerous fusiform cells are imbedded.

The *bloodvessels* of the bed of the nail form a coarse plexus in the corium of the matrix, from which vascular loops are given off to the papillæ; on the other hand, the proper bed of the nail has a much finer plexus, from which numerous thick vascular loops ascend into the ridges.

Numerous *medullated nerve fibres* lie in the subcutaneous tissue of the nail bed, and, losing their medullary sheath at about the level of the corium, run vertically to the surface. In one specimen prepared with chloride of gold, I followed such a nerve fibre as far as to the surface of the corium, from which the mucous layer had been detached in the act of preparation; I was unable to find any nerve fibres in the latter.

The upper surface of the dorsum of the wall of the nail is similar to that of the skin of the corium of the fingers; whilst its lower surface, that is turned towards the nail, is destitute of papillæ, is smooth, and contains no glands.

The *rete mucosum*, or *mucous layer of the nail bed*, differs in no respect from that of other parts of the skin. It fills up all the depressions of the nail bed, and the valleculæ between the papillæ of the matrix, as well as the furrows between the ridges, and is immediately continuous with the mucous layer of the adjoining skin, and with that of the nail fold. At the posterior angle of the nail fold the mucous layer of the nail matrix so fuses with that of the nail wall, as to form a wedge-shaped portion, which projects from the angle of the fold into

the corium that lies immediately upon the periosteum of the phalanx, and is firmly attached to it by short and tense connective-tissue fibres.

The deepest cells of the mucous layer of the nail bed are columnar, the intermediate ones are polygonal, whilst the most superficial are tabular. All enclose a large well-defined nucleus.

The further destiny of the cells of the mucous layers varies; on the proper bed of the nail they suddenly pass into flat epidermal scales, as in other parts of the skin; but on the matrix of the nail they pass gradually into the nail substance.

In vertical sections, dividing the nail into two lateral halves, it may easily be seen that the layer of nucleated flattened cells over the matrix of the nail is much thicker than over the nail bed, and that over the nail matrix they are continuous, by an oblique furrowed surface, with the horny nail substance. The thickness of this layer continuously diminishes towards the nail bed, whilst the thickness of the nail substance increases The line of junction between the mucous layer of the true nail bed and the nail substance, on the other hand, is sharp and level, a thin layer (in chromic-acid preparations) of looser epidermal scales existing in most cases between them, which also increases in thickness towards the free border of the nail (Reichert).

Between the mucous layer of the matrix and the root of the nail no sharply defined line exists, the uppermost flattened cells of the nail matrix passing continuously into still more flattened nucleated and distinctly contoured cells, colourable by carmine (Nagel), and these again into very flat scales, in which a nucleus is no longer distinguishable.

These scales are converted, in a plane falling off anteriorly towards the nail bed, into a homogeneous lustrous horny nail substance, that is no longer capable of imbibing carmine, but is deeply stained by chromic acid.

The mucous layer of the under surface of the fold of the nail that looks towards the nail is covered with an epidermal layer, increasing anteriorly in thickness, which is applied to the upper surface of the nail root, but can nevertheless be easily raised from it, and consequently plays no part in the formation of the nail.

The posterior part of the nail bed, provided with papillæ, and lying in the fold of the nail, must therefore be regarded as the exclusive seat of formation of the nail, and is properly termed the nail matrix.

It corresponds to the papilla of the hair, whilst the nail fold is equivalent to the hair follicle, and occasions the forward growth of the nail; for the nail cells, as they become more superficial, become constantly broader; but since they are unable

Fig. 204.

Fig. 204. Transverse section of a nail, made through the proper bed of the nail. *a*, Nail; *b*, loose horny layer beneath it; *c*, mucous layer; *d*, transversely divided nail ridges, with injected bloodvessels; *e*, nail fold, destitute of papillæ; *f*, the horny layer of the nail fold which has been deposited upon the nail; *g*, papillæ of the skin of the back of the finger.

to expand equably, on account of the posterior angle of the nail fold, they must necessarily press forward, and be pushed still further forward by those that succeed them.

It is on this account that the nail cells are arranged in an imbricated manner, the upper covering the greater part of the lower, and only leaving their posterior border free.*

Where the nail fold is deficient, *i.e.*, simply the nail wall, as frequently occurs with the little toes, the nail only increases in thickness, and forms a horny eminence, that attains a certain height, and then breaks off.

* Virchow, *Zur normal und pathologischen Anatomie der Nägel.* "On the normal and pathological Anatomy of the Nail." *Wurzburg. Verhand.*, Band v.

Inflammation of the matrix, attended with suppuration, leads to temporary or permanent loss of the nail, according to whether it is reproduced or altogether destroyed.

The new nail is formed by the matrix, and grows from behind forward over the nail bed. Suppurative inflammation of the proper bed of the nail causes no disturbance of the growth of the nail, and although it is frequently not again applied to the bed, it yet continues to maintain its normal thickness.

The nail itself, which is homogeneous in transverse section, or at most exhibits fine striæ, and refracts light doubly, is composed of nucleated epidermal scales intimately cemented together, but capable of being broken up by the action of various chemical agents.

According to Moleschott, ammonia dissolves the sparing amount of cement present in the nail cells in twenty-four hours. The cells form irregular polyhedra, and each includes a single round nucleus. Ammoniated oxide of copper in strong solution converts the scales into polyhedra in the course of an hour and a half, and in two or three hours they swell up to elliptical vesicles. These solutions rapidly attack the nuclei.

The best means of obtaining separate nail cells with distinct nuclei, is to macerate the nail for three or five hours in a 27 per cent. solution of potash. The nail soon becomes very soft, and it is only requisite to spread out a thin layer on the glass to obtain a satisfactory specimen.

The nail is finely and longitudinally striated, its surface exhibiting ribs that are not to be regarded as the expressions of the ridges of the nail bed (Kölliker), but as the result of the papillary structure of the matrix of the nail (Henle), since the nail root is also ribbed.

Development of the Nail.—At the third month of fœtal life we may observe a mound-like elevation of the skin, concave anteriorly, on the last phalanges, which corresponds to the nail fold, and results from the circumstance that at a line corresponding to the concavity of this elevation the mucous layer sends a wedge-like process into the tissue of the corium. This process consists of from two to three tiers of epithelial cells resembling those of the mucous layer.

In the fourth month we find, intercalated between the above, from three to four tiers of flat, nucleated, very sharply defined cells that correspond to the nail cells.

The portion of skin enclosed by this wall, which subsequently becomes the bed of the nail, differs at this time in no respect from the rest of the skin. At the fifth month the above-described nail cells introduce themselves between the mucous and horny layer of the nail bed, so that the previously formed nail is still covered by the horny layer, and has no free border.

As the nail extends below the horny layer to the tip of the finger in the sixth month, it raises the horny layer in the form of a pocket open behind.

CHAPTER XXVII.

SEROUS MEMBRANES.

By E. KLEIN.

The serous membranes in general are composed of an endothelium and a basement membrane or matrix, with lymphatics, bloodvessels, and nerves.

A. Endothelium.

The free surface of all serous membranes is covered by a single layer of cells. The mesentery, the serous portion of the diaphragm, and in part the external lamina of the pericardium, have an epithelium on both sides; whilst the parietal portion of the peritoneum, pleura, and dura mater have only a layer on that side that is turned towards the cavity of the sacs they form. As regards the external lamina of the pericardium, the cell investment is by no means complete, though in Rabbits, Cats, and new-born children it extends over a large, and in Guinea-pigs over the greater portion of the external surface.

Boehm (1) only admits the presence of a cell investment to the dura mater in the Rabbit. In the Triton and Frog, intervening between non-ciliated epithelial cells, on the parietal portion of the peritoneum, on the mesentery, and in the last-named animals, also on the abdominal surface of the wall (2) of the cisterna magna, isolated, small, ciliated, tesselated cells occur, together with groups of such cells.

The isolated cells are moderately flat, and possess a rounded or oblong, often excentrically situated, nucleus, the thickness of which often exceeds that of the cell, generally causing the

superjacent layer of cell substance to project at this point. The more regularly the cell is otherwise fashioned, by so much the more does the nucleus approximate the spheroidal form. The endothelium on the mesentery of the Rabbit is very regularly polyhedral, as is also that of the newly born child, that of the peritoneum investing the stomach and intestine of the Frog and Cat, and of the thoracic surface of the tendinous centre of the Guinea-pig.

Amongst the most irregular in form are the cells of the mesentery of the Frog, and in part also of the Cat. They are here always quite irregularly shaped, forming more or less elongated plates, constantly presenting irregular projections, and hence it results that the boundary lines of two adjoining cells are always more or less sinuous. The elongated cells of the two surfaces decussate in the direction of their length in the same manner as those of the opposite walls of a large lymphatic.

The nucleus of these endothelial cells rarely occupies a central position, but is usually oblong, and sometimes exhibits constrictions that affect either one half of the nucleus only, or its entire circumference; and indeed it is not infrequent to meet with elongated cells presenting several projections at the poles, and containing two nuclei.

On the pleura, the pericardium, and the central tendineum of the diaphragm, besides regular polyhedric cells, we meet also with more or less irregularly formed ones, presenting triangular and more or less elongated rhomboidal forms. The greatest variation also occurs in regard to the size of the cells and the extent of their periphery. Sometimes they are of the same magnitude over surfaces of considerable extent, sometimes a few groups of disproportionately small cells are found irregularly scattered, sometimes with and sometimes without intermediate forms. The latter arrangement is beautifully shown in the pericardium of the Cat, as well as on the pleura intercostalis (3), and upon the lymphatics on the abdominal surface of the peritoneum (4). The form of the endothelial cells, as exhibited in preparations stained with nitrate of silver, varies from point to point; but in the mesentery of the Frog and Cat, on the abdominal surface of

the centrum tendineum, upon the hereafter to be described fissures, and partially upon the inner surface of the external pericardial lamina of Rabbits, the contours of the endothelial cells present a remarkably well-defined sinuous character; and this occurs also, though only partially, on the pleura and the thoracic surface of the diaphragm. It is remarkable that in silvered preparations the cell contours over the subsequently to be mentioned broad fissures on the abdominal surface of the centrum tendineum, as well as upon the lymphatics of the pleura (5), are much more delicate than in the intervening spaces.

The arrangement of the endothelial cells is that polyhedric cells are simply juxtaposed, or where they are elongated their extremities are intercalated between those of the next row, or they are disposed radially, in groups of from four to ten, around a common centre. They are arranged in the last-named manner both upon the abdominal (6) and upon the thoracic surface of the centrum tendineum of the diaphragm, upon the mesentery, upon the abdominal surface (7) of the wall of the cisterna lymphatica of the Frog, upon the pleura (8) and upon the internal and external surface of the pericardium of the Rabbit, Cat, and of Man, as well as upon the dura mater of the Rabbit (9).

In the centre of these endothelial groups we find one or several (two or three) sharply defined, rounded, or triangular spaces of various size, which, since the time of Recklinghausen and Oedmanson, have been regarded as apertures between the endothelial cells, or as the so-called stomata.

On the other hand we meet also in these places with radially arranged groups of endothelial cells, in the centre of which none of the above-mentioned stomata can be found. Considering that in silvered preparations minute but variously sized areas, either isolated or in small groups, and always sharply defined, occur between two or several endothelial cells, and that in certain spots, on account of the proximity of figures of very various size, and of the absence of nuclei, it appears to be quite impossible to decide what is a stoma and what a small endothelial cell, all inquirers have held the demonstration of the existence of spaces between the endothelia in such preparation to be incomplete. The above-described images,

however, are accepted as stomata on the ground of the experiments (10) of Recklinghausen, subsequently repeated by Ludwig and Schweigger-Seidel, Dybkowsky, Schweigger-Seidel and Dogiel, and Böhm. The successful injections of Dybkowsky also tell strongly in favour of the existence of stomata. (See fig. 8 in his treatise.)

From an histological point of view, those small figures can alone, strictly speaking, be regarded as stomata that occur in the centre of radially arranged and relatively large endothelial cells in such situations. With a little care we may find in most cases, as Schweigger-Seidel and Dogiel (10) have pointed out in the instance of the abdominal or external surface of the wall of the cisterna lymphatica magna, that the nuclei of the endothelial cells surround the supposed stoma, and lie close around its periphery. All other small areas, whether isolated or aggregated into groups of two or three, in all probability only correspond to young cells proceeding from the fission of larger ones. This view is supported first by the presence of bi-nucleated cells, as in those of the mesentery of the Frog, where the nuclei have undergone fission; secondly, by the peculiarly irregular form of the endothelial cells in question, which have precisely the appearance of having undergone changes in form during life; thirdly, by the circumstance above alluded to, that here and there between individual larger several small cells are introduced; and lastly, by the discovery of Ludwig and Schweigger-Seidel, that on the abdominal surface of the centrum tendineum of the Rabbit all stages of the division of the nuclei in the endothelial cells may be witnessed. Ludwig and Schweigger-Seidel regard the cell groups resulting from the division of the endothelial cells as lymph corpuscles.

I must still mention the cellular investment of the omentum majus of the Cat. This consists of a very delicate framework of connective tissue, with fissures that diminish in size towards the larger fasciculi supporting the bloodvessels.

The endothelium here closely invests the trabecular framework.

The methods already described of silvering and maceration in iodine-serum are best adapted for its display.

B. The Matrix.

The stroma of the serous membranes is composed of connective and elastic tissue. The former consists of undulating fibres united into fasciculi, which form in general a delicate trellis-work interweaving with each other in various directions, and forming at certain points thicker trabeculæ in which the larger bloodvessels and lymphatics, as well as nerve trunks, lie imbedded. The connective tissue is thus arranged in the mesentery, in the delicate and sparing subserous tissue of the pleura (12), and in the similar tissue covering the abdominal and thoracic surfaces of the centrum tendineum. On the other hand, the layer of connective tissue may present a more tendinous appearance, as on the centrum tendineum itself, where in the Rabbit there is on the thoracic surface a circular, and on the abdominal a radially arranged, layer (13), and in part also in the pericardium, in the deeper layers of the pleura intercostatis, and in the dura mater.

A close plexus of very fine elastic fibres runs through this framework of connective tissue, the fibres being for the most part straight or slightly undulating, more rarely strongly looped or spiral. The amount and number of layers of these plexuses of elastic fibres are very variable, being largest in the mesocolon of Mammals and of Man, and in the mesentery of the Guinea-pig, always abundant in the mesentery of the Frog and of Mammals, in the pleura, in the matrix lying superjacent to both the radial and the circular tendinous layer of the centrum tendineum of the diaphragm, and in the pericardium.

A variable quantity of adipose tissue is found in the mesentery and in the pericardium; in the former it is chiefly found in the larger trabeculæ and their subdivisions that run radially from the root of the mesentery towards the intestine, corresponding to the course of the larger bloodvessels. Here, as elsewhere in the masses of connective tissue, numerous cellular structures are to be found distributed between the fibres. Such are branched cells with rounded nuclei, forming a close plexus by means of their simple or branched protoplasmic processes; various-sized rounded or irregular granulated masses of protoplasm, containing one or several nuclei; fusiform granular

cells with rounded or oblong nuclei (frequently intervening between the straighter fasciculi of connective tissue of the middle layer—radiating and concentric layer—of the centrum tendineum, the deeper layers of the intercostal pleura, the outer lamina of the pericardium and of the dura mater); and lastly, vagrant or migrating cells. In many Vertebrata the tissue of the peritoneum contains isolated and retiform fasciculi of smooth muscular fibres; these are especially abundant in the mesentery of the Triton and of the Frog. They are less numerous in Mammals, though even here there are certain regions where they are present in considerable abundance, as in the peritoneal investment of the stomach of the Rabbit.

The examination of the fibrous elements of the serous membranes may best be conducted on thin sections (as of the pleura, 14, and diaphragm, 15) that have been hardened in chromic acid, or by means of surface views of portions of the membranes (mesentery, pericardium), either in the fresh state, or after having been previously macerated in bichromate of potash. For the study of the cellular elements we possess an admirable agent in chloride of gold, though here also the examination of fresh preparations must not be neglected.

c. Lymphatics.

The presence of lymphatics in the connective tissue of serous membranes was called in question by Dybkowsky, Schweigger-Seidel, and Ludwig and Schweigger-Seidel, but Böhm discovered them upon the inner surface of the dura mater; later inquirers also consider the statement made by Schweigger-Seidel (13), that the appearances of lymphatics is the result of manipulation in an albuminous layer of cementing tissue between the endothelium and matrix, is negatived by the fact, which indeed is perfectly true, that in some cases the endothelium may be seen to be completely preserved over the appearances of lymphatics presented by the matrix. I am able, personally, so far as regards my own observations on serous membranes,—namely, upon the mesentery of the Triton, Frog, Rabbit, Guinea-pig, Cat, and Man; the parietal layer of the Peritoneum of the Frog, Rabbit, and Man; the pericardium, pleura, and upon both the

thoracic and abdominal surfaces of the centrum tendineum of the Rabbit, Guinea-pig, Cat, and Man,—fully to corroborate the statements on the serous membranes made by v. Recklinghausen. (See the woodcuts 57 and 58, in chapter viii. of this work.)

According to Dybkowsky, the pleura costalis only possesses lymphatics in the intercostal spaces, and where it is applied to the musculus sterno-costalis. The capillary lymphatics here form a close plexus, from which small trunks containing valves arise, that run to the margin of the intercostal space. The capillary plexus is for the most part arranged in two layers, one of which is superficial, and occupies the fissures and spaces of the matrix, their cavities being separated from that of the pleura by the endothelium alone, and into which the stomata found between the endothelial cells directly open (19); whilst the other is more deeply situated, and separated from the former by connective tissue, the fasciculi of which run parallel to the plane of the pleura; both layers intercommunicate freely. The portions that cover the ribs themselves possess no lymphatics. The mediastinum has lymphatics at those points only at which adipose tissue intervenes between its laminæ.

The lymphatic capillaries of the external lamina of the pericardium form a close plexus lying near its inner surface, and receiving serous canals from all parts of the matrix. According to Ludwig and Schweigger-Seidel, we may distinguish in the tendinous centre of the diaphragm of the Rabbit a system of wide lymphatics that lie parallel to one another between the fibres of the radiating layer, and are lined by endothelium; they are covered by the basement membrane of the abdominal surface, which consists of strong trabeculæ corresponding to the spaces intervening between the fissures, whilst from the latter more delicate fasciculi arise, which form a delicate network over the lacunæ themselves (20).

From these lacunæ of the lymphatic system canals extend towards the thoracic surface, where a close but delicate network of capillary lymphatics exists between the pleura and the circular layer. This plexus again pours its contents into wide lymphatics provided with valves, that are likewise situated on the thoracic surface. The plexus of capillary lymphatics

attains its greatest development at the posterior part of the centrum tendineum.

In addition to these statements made by Ludwig and Schweigger-Seidel, it may be observed that in the Rabbit, Man, and Cat, but especially in the Guinea-pig, a rich system of serous canals and lymphatic lacunæ, lined with endothelium, can be demonstrated in the matrix itself, both on the abdominal and thoracic surfaces, by treatment with nitrate of silver. On the abdominal surface of the centrum tendineum of the Guinea-pig we find that, from the trabeculæ of the matrix containing bloodvessels and nerves, smaller trabeculæ, corresponding to the divisions of the bloodvessels, are given off tolerably rectilinearly, separated by large wide fissures lined with epithelium. (See vol. i., fig. 58, p. 317.)

These lymphatic cavities receive on all sides the short lacuniform serous canals, as well as the longer and narrower vessels that run in the larger trabeculæ with bloodvessels and nerves, and that are also in fact developed in the adventitia of the former, and in the wide connective-tissue sheaths of the latter.

These very wide lymphatic spaces communicate with the fissures lined with epithelium, situated between the several layers of the tendinous tissue.

In the mesentery the larger lymphatics provided with valves are situated in the principal trabeculæ that pursue a radial course from the root towards the intestinal border of the membrane, and receive from all sides both small and large capillary lymphatics, which, in the mesentery of the Frog, sometimes originate in rounded or oblong wide lymph spaces that are lined with epithelium, and sometimes proceed from the serous canals themselves. The wide lymph spaces take origin from the rhombic, stellate, or lacuniform serous canals, and occupy the interspaces of the smaller trabeculæ of connective tissue that extend between the radially arranged chief trabeculæ, and intercommunicate by many smaller arched branches.

In the mesentery of the Frog, as well as on the abdominal surface of the centrum tendineum of the Guinea-pig, bloodvessels and nerves can here and there be distinctly seen imbedded in lymphatic cavities, whilst in other parts they are accompanied on both sides by capillary lymphatics.

It remains to be mentioned that in specimens of the tunica adventitia both of the blood and of the larger valved lymphatics of the mesentery of the Frog, prepared with nitrate of silver, a beautiful pattern appears, presenting the closest similarity to the distribution of the serous canals.

For the study of the lymphatics of the serous membranes, the best means that can be adopted is the examination of objects impregnated with silver, and pencilled, or still better unpencilled, and specimens self-injected from the serous cavities.

For more minute details the reader is referred to the excellent works of Recklinghausen, Dybkowsky, Ludwig, and Schweigger-Seidel.

D. BLOODVESSELS.

The capillary bloodvessels, as Dybkowsky has shown, form wide plexuses in the intercostal and sterno-costal pleura, the larger branches being accompanied by lymphatics. The capillaries of the pleura communicate freely with those of the fasciæ as far as to the commencement of the muscular tissue. That portion of the pleura that covers the ribs frequently appears to be particularly well supplied with blood capillaries.

In the parietal lamina of the pericardium the larger bloodvessels penetrate from without, and break up towards the inner surface into a tolerably close capillary system.

In the mesentery the larger trunks running radially from its root towards the intestine, branch in an arborescent manner, giving off smaller and still smaller twigs, and ultimately losing themselves towards the surface in a wide-meshed capillary expansion.

In the centrum tendineum of the Rabbit the larger vessels, according to Ludwig and Schweigger-Seidel, enter for the most part from the thoracic surface to reach the deeper portion of the serosa, and more rarely from the abdominal surface; the smaller branches penetrate through the tendinous substratum, and run in the spaces between the fasciculi of the radiating fibrous layer; to the borders of these they appear to be adherent, not by means of their adventitia, but by a delicate membrane extending over them. The capillaries of the matrix of the thoracic and abdominal surfaces form a wide-meshed plexus.

The bloodvessels of the dura mater consist, according to Recklinghausen (21), and Böhm (22), of a venous plexus situated on the external surface, the branches of which are disproportionately large. In the Dog in particular the venous branches coalesce to form large sinus-like spaces between the arteries. Böhm has observed these venous plexuses become filled from the inner surface of the dura mater, and is therefore of opinion that a free communication exists between the veins of the external surface of the dura mater and those of the serous cavity of the cranium.

The bloodvessels may be followed and studied, even in their finest ramifications, by means of injections, and in specimens prepared with silver and gold; the latter mode of preparation in some instances permits injections to be entirely dispensed with.

E. NERVES.

The nerves supplying serous membranes have received but little attention. According to Cyon (23), the nerves distributed to the septum between the peritoneal cavity and the cysterna lymphatica magna of the Frog are doubly contoured, and run in small fasciculi of two or three enclosed in a separate sheath. After undergoing subdivision to a greater or less extent, they lose their medulla, and form fibres that bulge at intervals from the presence of nuclei.

At those points where a fasciculus breaks up, broad nucleated fibres appear, that possess a distinctly fibrillated structure.

The several fibres, by their crossing and mutual entwining, form a plexus with rhombic meshes of various size. Cyon considers that this plexus is not terminal, but that the fibres end in the tissue by free extremities.

The nerves entering the mesentery are composed of medullated fibres, one or two of which accompany the larger bloodvessels. Both the isolated fibres and the fasciculi pursue a well-marked wavy course.

The few branches given off laterally as they pass outwards are composed of one or two non-medullated fibres, also characterized by the presence of projecting nuclei at intervals; ultimately the individual non-medullated fibres form a rhombic-

meshed plexus that is particularly close in the vicinity and in the substance of the adventitia of the larger bloodvessels (in the Frog), and exhibits oblong nuclei at the nodal points.

I have been unable to follow out the large fasciculi of non-medullated fibres in the serous layer covering the peritoneal surface of the centrum tendineum; these are characterized by knot-like enlargements, and, like those found in parts of the mesentery, appear to be separated from the adjoining tissues by a moderately wide lymphatic space.

The silver method of impregnation is well adapted for the examination of the nerves, though even this is surpassed by the plan of tinting them by means of solution of chloride of gold.

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10. See chapter viii. of this work.
11. *Loc. cit.*

12. Dybkowsky, *loc. cit.*, fig. 8, 20.
13. Ludwig und Schweigger-Seidel, *loc. cit.*
14. Dybkowsky, *loc. cit.*
15. Ludwig und Schweigger-Seidel, *loc. cit.*
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18. *Loc. cit.*
19. Dybkowsky, *loc. cit.*, fig. 8.
20. Ludwig und Schweigger-Seidel, *loc. cit.*, fig. 8.
21. Die Lymphgefässe und ihre Beziehung zum Bindegewebe, *loc. cit.*, p. 71. (The Lymphatics, and their relation to connective tissue.)
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CHAPTER XXVIII.

THE MAMMARY GLANDS.

By C. LANGER.

THE glands destined for the secretion of milk, the tissues of which for the most part only attain their complete development, and their capacity for functional activity, after puberty, present *club-shaped gland vesicles*, situated at the extremities of a ramified system of ducts. The fifteen or twenty *excretory ducts* open separately on the *nipple* as fine tubules, after they have previously formed in the region of the areola dilatations, constituting milk receptacles, or reservoirs, the sides of which project irregularly according to the number of the branches they give off. A few of the latter pursue a recurrent course, in order to receive the secretion of the lobules situated beneath the areola. Some of these glandular granules, however, give off fine excretory ducts that run to the surface of the areola, and open on the small projections of its surface, thus appearing like small copies of the proper nipple (glandulæ aberrantes of Montgomery). Anastomoses, if they occur at all between the branches of two ducts, are very irregular, and are met with only in the vicinity of the reservoirs.

The entire mass of closely compressed terminal vesicles form *small lobules* that, at the lower surface and borders of the gland, hang in pairs from the extremities of each dichotomously divided duct; but near the centre of the gland, and beneath the areola, constitute small isolated lobules that are not unfrequently seated immediately on the lateral wall of one of the large ducts. These small lobules never coalesce to form larger

ones, nor can the whole gland ever be broken up into large lobules, corresponding to the several excretory ducts, because the *stroma of the gland* is composed of a firm and undivided mass of connective tissue, that only becomes somewhat looser near the periphery, in order to invest and isolate the lobules of the gland that are there present. Lamellæ of the stroma, given off from the margins and upper surface of the organ, join with the subcutaneous connective tissue to form nooks and capsules that are occupied by the surrounding fat. The solid nucleus of the gland, therefore, is in immediate union with the skin only at the nipple; at this point, and beneath the areola, no adipose tissue exists, but in its place there is a thick layer of smooth muscular fibres.

The structure of the excretory ducts is very simple; their walls consisting of finely fibrous connective tissue, which is more dense externally, with a circular disposition of the fibres, the outermost layer being intermingled with many elastic fibres. They have no proper muscular system; their epithelium is composed of small columnar cells. The larger ducts, when empty, collapse, the thin walls falling into longitudinal folds, which give them an irregularly distended or stellate form on section.

The gland vesicles are lined by a single layer of epithelium, which at their fundus is composed of small polyhedric cells, but near their neck of somewhat higher cells that sometimes bound a very small central space. The entire cavity of the acinus is filled with fat drops, the anatomical constituent of the milk; and although the contents of these acini are easily removed, many fat drops always remain adherent to the epithelium, and some may even be found distributed between the nuclei of the epithelial cells. In puerperal women who have died soon after delivery, the gland vesicles contain a few milk spheroids sparingly interspersed amongst the closely compressed epithelial cells. If the fat be extracted from the contents of the acini by means of æther, a plexus traversing the acinus in all directions is formed by the coagulated caseous substance with spaces corresponding to the fat drops that have been removed. Connective tissue constitutes another element of the wall of the acini, and with its cellular

texture interspersed with nuclei and processes forms a little cradle surrounding each of the gland vesicles, which becomes visible after the detachment of the epithelium. These form the structural elements that have been already demonstrated by Boll* in the lachrymal and salivary glands. It is easy to show the continuity of this plexus with the inter-alveolar

Fig. 205.

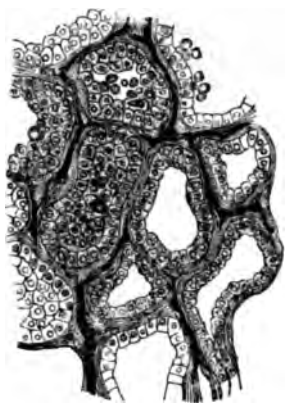

Fig. 205. Section carried through the terminal vesicles of the gland of a nursing Woman. System 8, Hartnack.

trabeculæ, but I have not been able to satisfy myself that processes are given off from it, to or between the epithelial cells, and I must leave undetermined the relation that the apparently perfectly structureless membrane, which is made apparent by maceration of the lobules, bears to this plexus.

All the large vessels supplying the gland run in the subcutaneous connective tissue, whilst those entering the deep surface are small. As the former run towards the nipple, they give off branches at intervals, some of which penetrate the substance of the organ, whilst others are distributed to the skin. The ultimate ramifications of these trunks, on reaching the base of the nipple, give off both ascending and descending branches. The arterioles distributed to the parenchyma of the gland do not always run in company with the ducts, and

* Max Schultze's *Archiv*, Band v., p. 332.

for the most part branch quite independently of them, and hence it comes to pass that the small lobules of the gland give off and receive their vascular supply at all parts of their periphery. The capillaries of the small lobules form plexuses of three dimensions (cubic), containing the acini in their rounded or polygonal meshes. In thin sections, consequently, they are seen to run in their slender inter-alveolar trabeculæ. It may easily be demonstrated that the capillaries of each lobule form a closed plexus, only communicating with those of the adjoining lobules by the small arteries and veins.

Fig. 206.

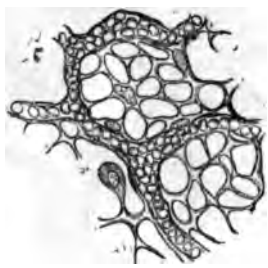

Fig. 206. Reticular connective tissue from the wall of two acini, with a few epithelial cells. System 9, immersion, Hartnack.

The capillary vessels, again, supplying the ducts are quite distinct from those of the stroma, and consist of fine tubules that inosculate to form elongated meshes surrounding the large ducts of the nipple in the form of a tolerably close, yet very delicate, plexus. Vascular arrangements resembling those of the erectile tissues do not, therefore, occur in the nipple; for neither the vessels of the stroma, nor those of the muscular tissue, present any unusual calibre. The capillary loops of the papilliform bodies of the areola proceed likewise from special trunks running immediately beneath them, and giving off elongated arches into their substance. The veins of the nipple form an annular chain of anastomoses beneath the areola,—the well-known circulus Halleri.

Nothing is at present known in respect to either the lymphatics of this gland, or of the mode in which the nerves distributed to it terminate.

The first rudiment of the gland becomes visible about the third month of intra-uterine life, yet in the newly born child we rarely find anything more than the principal ducts, with some indications of ramification, in the form of two or three club-shaped processes; and even if these be somewhat more developed, the terminal vesicles are always absent, even in those cases where a fluid is excreted; but numerous and closely approximated dilatations then occur, that give to the gland the appearance of a group of sebaceous follicles.

The ducts continue to increase up to the *period of puberty*, though only slowly even in the girl; but they then undergo rapid development, the condition attained remaining persistent in the female, whilst in boys it may undergo regressive metamorphosis. In the *adult male*, as a rule, only some of the principal ducts are present, with a few slightly subdivided projections; but cases also occur where the glands, having attained the size of a walnut, contain a ramified system of ducts, presenting forms similar to those of the girl before the period of puberty.

True acini, constituting the extremities of an already highly ramified system of ducts, occur only in the sexually *mature female*. At this period of life the gland usually already exhibits the grape-like acinous structure, though the lobules are small, widely separated from each other, the ducts of narrow calibre, and the vesicles small, and more of a cylindrical than of a clavate form. The contents of the entire system of secretory ducts in the young woman consist of collections of cells, which, densely packed, form solid masses at their extremities; whilst in the ducts, which are already pervious, they form a single layer, lining the inner surface. Finely fibrillated connective tissue enters into the composition of the walls of the larger ducts, but those of the smaller are formed of a layer of hyaline tissue, swelling strongly in water, and separated from the stroma on its outer surface by a series of attenuated fusiform corpuscles. At the extremities of the ducts this layer appears much thicker, and presents, in transverse sections, broad swollen haloes, or zones, in close approximation to each other by their external sharply defined contours, whilst the internal border exhibits fine inflections, with projecting folds, that are evidently due to the imbibition of fluid by the membrane.

The stroma of the developing gland consists of tendinous fasciculi of connective tissue with scattered fusiform corpuscles that are so closely interwoven with each other as to form an indivisible, dense, caoutchouc-like mass, with numerous canals for the passage of the ducts and larger bloodvessels. Capillaries arranged in the form of interwoven plexuses everywhere traverse the compact tissue, but principally run towards the

Fig. 207.

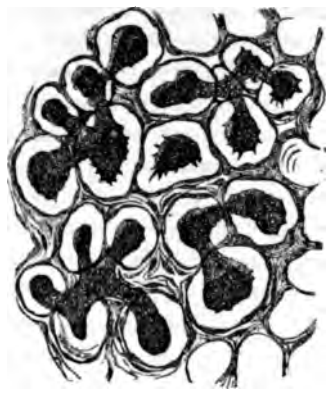

Fig. 207. Acini of the mammary gland of a young Woman, with greatly swollen haloes. Hartnack's system No. 8.

ducts. The blunt extremities of the still growing ducts become surrounded by fasciculi of vessels, which ramify on the surface, and, closely applied to each, accompany it for some distance in its course. In these cases the vessels form fibre-like appendages that obviously prefigure the direction of the subsequent growth of the ducts; the lobules already present, on the other hand, are surrounded and traversed by a plexus of capillaries.

Many of the capillaries of the stroma are abundantly supplied with nuclei; from others, again, very fine processes are given off that are scarcely pervious, and clearly represent capillaries in course of development. I have also been able to distinguish small nerves composed of two or three medullated fibres, and I have seen fibrils pursuing an isolated course, and dividing dichotomously. In the interior of the vascular fasciculi given off from the obtuse ends of the ducts I have

further observed certain kinds of fine fibres which it was impossible to follow further, and which appear to terminate at the outer surface of the hyaline layer, but I was unable to ascertain whether these were nerve fibrils or not.

Fig. 208.

Fig. 208. Terminal dilatations of the ducts of the mamma in a Girl fourteen years of age. System 4, Hartnack.

From all this then it would appear that the process of formation of the glandular elements may be correctly regarded as a continuously progressive budding, and it is scarcely possible to doubt that it is immediately dependent on a proliferation of the epithelial cells; it is also certain that in proportion as the system of ducts proceeds to form acini, the intervening dense stroma becomes gradually looser in texture and diminished in quantity, though the causative relations of these two processes may be scarcely capable of histological definition. It is yet worthy of observation that, coincidently with the formation of the acini, fat cells make their appearance in the stroma, which are unquestionably to be regarded as a secondary product of these processes.

The changes that take place in pregnancy, preparatory to the active performance of the function of the gland, consist, in the first place, in an increase of the secreting surface. The acini, with the ducts, become wider, the hyaline layer of the walls thinner; fat vesicles appear in their interior, at first few in number, and only in the centre of the cell masses, but subsequently in such quantities that they entirely fill the dilated and bulbous terminations of the ducts that have in the meanwhile undergone great augmentation in size, and compress their epithelial lining closely against the wall. The interlobular connective tissue becomes constantly looser, and contains more and more fat, and the dense part of the stroma diminishes in quantity, though it never altogether disappears, since even in nursing women it forms a solid nucleus in the centre of the gland. As these changes do not occur quite simultaneously in all parts of the gland, an opportunity is afforded in puerperal women dying shortly after delivery, to observe many transitional forms of the acini.

It cannot be doubted that the fat vesicles, which constitute the morphological elements of the milk, proceed from the epithelial cells of the acini; for, in the first place, the first visible oil drops appear in the very centre of the epithelial masses, whilst again, in the milk first secreted (colostrum) spheroidal nucleated cells occur, distended with fat vesicles, and, lastly, in the acini of the gland in nurses, not only isolated, but serially arranged groups of cells may be found filled with oil drops. I have met with cells containing several small fat molecules, and with others containing a nucleus around which a crescent of larger molecules had been deposited. In serially arranged cells containing oil drops these occupy that portion of the cell which is directed towards the cavity, whilst the nucleus is situated nearer to the wall of the acinus. This explains why the walls of empty acini not unfrequently appear to be still beset with fat vesicles. Clearly these represent epithelial cells that have been distended and have burst, allowing the fat drops to escape. It is still questionable whether such epithelial cells die and are immediately replaced by others, or are capable of producing a succession of fat molecules. The latter is perhaps the correct view, and is, at all events, in accordance with the observations

of S. Stricker,* who is of opinion that the detached colostrum cells swimming in fresh milk excrete fat molecules.

The *regressive metamorphosis* of the parenchyma appears to commence as soon as the gland is no longer required for nursing. In a nursing woman, who died after an illness of three weeks' duration, I found the follicles of the gland already shrunken and condensed, and once more separated from each

Fig. 209.

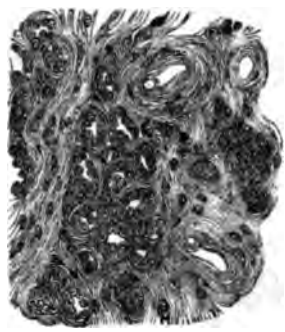

Fig. 209. Acini and stroma from the mammary gland of a nursing Woman who had died after three weeks' illness. System 8.

other by broad septa of connective tissue containing but little fat; the acini were small, and no longer contained oil drops, whilst the epithelial cells were in some parts collected into irregular heaps, and in others were scattered over the walls; the ducts, however, were everywhere permeable to injection, even to their ultimate ramifications. The larger ones contained a tenacious brownish material intermingled with fat molecules. The mammary gland of a Bitch presented precisely the same appearances three weeks after delivery.

I have found similar conditions of the parenchyma of the gland in a healthy female who had had no child for a long time previously, and they must therefore be regarded as representing the *inactive state* of the organ. At the same time it is quite possible that the regressive metamorphosis

* *Wiener Academ. Berichte*, Band liii.; Abtheil ii., p. 184.

may, in many cases and in many parts of the gland, proceed to a much greater extent, since in the gland of this same woman I observed, around a few wide ducts, numerous though short and closely compressed pullulations. Speaking in general terms, small terminal processes, or acini, attached to dilated ducts, indicate foregone pregnancy. So much is certain, that healthy, well-nourished married women preserve the acini of the gland often with the same characters as are presented by young women, except that the hyaline sheaths are absent.

Complete atrophy of the acini occurs about the period of the *grand climacteric;* the dense fibrous stroma also dis-

Fig. 210.

Fig. 210. From the mammary gland of an old Woman, ninety years of age, showing the extremities of the ducts, partly in cross section; the stroma with a few capillaries and many elastic fibres. System 8.

appearing altogether. The whole mass of the gland is shrunken, and forms a membrane-like thin disk, adherent to the nipple, and surrounded by fat on both sides. In the remains of the gland the ducts alone are visible, that sometimes still exhibit fine ramifications that may be regarded as intralobular. These ultimate processes of the ducts are of cylindrical form, end blindly, without further appendages, are very thin-walled, are all for the most part collapsed, so that they appear like fissures when divided transversely, and are lined internally by a single layer of flattened epithelium. The contracted ducts are united together by loose fibrous connective

tissue, containing a considerable quantity of elastic fibres and many chains of fat cells.

For the investigation of the coarser ducts the corrosive injecting fluids are generally employed. Sometimes the fluids penetrate so well in the case of the glands of young people, that the ducts may be followed to their ultimate ramifications. Glands that have been hardened in spirits of wine, or boiled in pyroligneous acid, are well adapted for the purpose of exhibiting the budding forth of the young ducts, their structure, and the characters of the stroma. In pyroligneous acid preparations, the arrangement of the muscular tissue and of the papillary projections of the nipple may be readily investigated. Instructive preparations for the examination of the epithelial cells in the acini may be obtained from specimens that have been hardened in chromate of potash or absolute alcohol. Staining the lamellæ with carmine also renders apparent the fine contours of the epithelial cells, whilst perosmic acid blackens the smallest particles of fat contained in their interior. The injection of the bloodvessels can usually be effected even in mammary glands that have been removed by operation, providing Hering's apparatus and very fluid injections are employed.

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CHAPTER XXIX.

THE EXTERNAL GENERATIVE ORGANS OF THE MALE AND FEMALE, WITH THEIR GLANDULAR APPENDAGES.

By E. KLEIN.

A. Male Organs.

I. Vas deferens.—The vas deferens is a structure containing a considerable quantity of muscular tissue, and is essentially analogous in its structure to the excretory ducts of the larger glands. It consists of a mucous membrane, a muscular tunic, and an external loose investment of connective tissue, the tunica adventitia.

The internal surface of the *mucous membrane* is lined with an *epithelium* that offers in the adult, and still more in the newly born child, manifold varieties. At the commencement of the vas deferens of the adult it consists for the most part of a single layer of ciliated columnar cells. The individual cells are either conical or cylindrical, about 0·03 of a millimeter in length, with a roundish or oblong nucleus, containing distinct nucleoli; occasionally fusiform cells are found interspersed amongst the conical, so that a laminated columnar epithelium results. The conical cells are furnished with very short fine cilia, both where the epithelium is arranged in only a single layer, and where it is laminated.

The point at which the most superficial cells lose their cilia varies, and is not the same for the whole circumference of the tube; according to my observation, however, no such cells can ever be found at a distance of four centimeters ($1\frac{1}{2}$ inch) above the epididymis.

In adults the epithelium remains tolerably uniform throughout the rest of the tube, except that many cells present a distinctly marked striated basal hem or border. In the child there is a great difference between the epithelium lining the extra- and the intra-abdominal portions of the duct. In the former the epithelium is for the most part laminated, one or two layers of polyhedric and spheroidal cells lying subjacent to a superficial layer of short columnar cells. Both of these sets of cells contain a relatively large and usually spheroidal nucleus. In that portion of the vas deferens, however, contained in the abdomen, the epithelium resembles that of the adult, the cells being beautifully defined and elongated, or conical, with a border composed of rods. They are either arranged in a single layer or, which is more common, they are separated by fusiform cells pressing in amongst them from without. The thickness of the epithelial layer in the newly born child and in the extra-abdominal portion is about 0·02 of a millimeter, and in the intra-abdominal part about 0·03 of a millimeter. Near the ampulla (dilatation just above the prostate) of the vas deferens, the epithelium increases slightly in thickness.

The *mucous layer* succeeding to the epithelium presents two or three longitudinal folds, that in the ampulla and their vicinity are not only of considerable height, but are also more numerous. They are here also connected by a few transverse plaits, so that hollows are formed, which some observers (Henle, Leydig) have described as glands. The mucous layer is composed of connective tissue and elastic fibres. The former consists of decussating fasciculi of fibres, that externally run chiefly in a horizontal direction, but near the epithelium are more oblique, and are lost as they pass upwards or downwards.

The elastic fibres form a tolerably dense plexus, and like the fasciculi of the connective tissue of the mucous layer are continuous externally with the septa of the muscular bundles, and through these septa with the loose adventitia.

The thickness of the mucous membrane depends on the thickness of the *muscular tunic*, to which it bears an inverse relation. The latter, with the exception of the first part of the vas deferens, is essentially composed of two layers, arranged at

right angles to each other—an internal circular, and an external longitudinal. Both consist of unstriated muscular fibres alone. At the commencement of the vas deferens, and extending to a distance of two centimeters (three-fourths of an inch) from the epididymis, there is always an internal longitudinal layer, but elsewhere this is only represented by a few fasciculi lying internally to the circular layer.

Fig. 211.

Fig. 211. Transverse section made through the commencement of the vas deferens of an adult. *a*, Epithelium; *b*, mucosa; *c*, internal; *d*, middle; *e*, external muscular layer; *f*, fasciculi of the cremaster internus; *g*, a vein with muscular walls. Magnified with Hartnack's objective system No. 2, ocular 3.

In adults the thickness of this internal longitudinal layer varies from 0·06 to 0·1 of a millimeter. The thickness of the middle circular layer diminishes from the commencement of the vas deferens towards the ampulla, but at this part it re-acquires its original thickness, amounting to about 0·5 of a millimeter. The muscular layers in the newly born child are

thinner than in the adult. Wherever an internal longitudinal layer is present, scattered fasciculi of smooth muscular fibres from it penetrate, obliquely and longitudinally, into the mucous layer, and are to be met with immediately beneath the epithelium. Moreover the outermost fasciculi of the circular layer decussate with those of the longitudinal at many points, as may be particularly well seen at the ampulla and adjoining part. Many fasciculi of the external longitudinal layer here dip into the circular, in which, after pursuing an oblique course for some distance, they terminate.

On one side of the tunica adventitia of the vas deferens, and arranged almost in the form of a semi-circle, are a series of longitudinal fasciculi, more or less separated from one another, of smooth muscular fibres that have been denominated the cremaster internus by Henle. These muscular fasciculi are in many parts in such close apposition to the external muscular layer of the vas deferens, that it is impossible to separate them.

The cremaster internus is most strongly developed at the commencement of the vas deferens, and progressively diminishes in thickness towards the point of its entrance into the abdomen, though it increases laterally to such an extent that isolated longitudinal fasciculi of smooth muscular fibres may be found around the entire periphery of the adventitia.

The *nerves* form a tolerably dense plexus—the plexus spermaticus—situated on that side of the tunica adventitia which is opposite to the cremaster internus. The fibres of which the trunks are composed are everywhere medullated. The sheath usually sends processes into the interior of the nerve, dividing it into two or three subordinate fasciculi. These, perhaps, correspond to the various origins from which the trunks obtain their fibres, as it is well known that the nerves entering the plexus spermaticus proceed both from the spermatic nerves and the sympathetic. The smaller twigs given off from the spermatic plexus penetrate the muscular tunic and the mucous layer of the vas deferens, and may be everywhere traced as medullated fibres.

Small ganglion cells are found scattered in the upper parts of the vas deferens, both in the nerves of the spermatic plexus and in the more externally situated and quite isolated trunks.

Near the ampulla completely formed ganglia exist of spheroidal or oblong form, having a diameter of about 0·35 of a millimeter.

The sheath of the ganglia consists of ordinary fibrillated connective tissue, with interspersed fusiform cells. A few fibres penetrate from the periphery into the interior of the ganglia, and unite with a cell network that is extended through this substance. The ganglion cells found in the ganglia are small, provided with two or three processes, and contain a relatively large, sharply defined, clear nucleus, with distinct nucleoli. Each ganglion cell occupies a nucleated capsule, which, as elsewhere, is composed of connective tissue continuous with the sheath of the nerve fibres joining the cells.

The plexiform structure in the interior of the ganglia above referred to, only presents distinct nucleated granular cells at its nodal points in newly born infants.

In the ampulla, and in the vas deferens beyond this point, the ganglionic enlargements contain, besides small ganglion cells, having a diameter of 0·0014 of a millimeter, numerous larger ganglion-cells 0·03 of a millimeter in diameter. Both forms possess a nucleated capsule.

Externally to the nervous plexus, which is usually situated at one side of the vas deferens, is a plexus of *veins* known by the name of the plexus pampiniformis, as well as a few small *arteries*. This system of vessels communicates with the proper vascular system of the vas deferens, of which the rich capillary supply of the muscular tunics and the subepithelial plexus of the mucosa are especially worthy of notice.

The thickness of the walls of the smaller veins of the plexus pampiniformis, and their distinct subdivision into three layers, are remarkable; of these layers the internal contains elastic fibres and isolated longitudinal muscular fasciculi, the middle circular muscular bundles, whilst the external is a tunica adventitia composed of more loosely arranged longitudinal muscular fasciculi.

Still more externally, on that side of the vas deferens opposite to the cremaster internus, smaller longitudinal muscular fasciculi of smooth muscular tissue are met with, forming a layer that may be named the cremaster medius. The spermatic

cord is richly supplied with thin-walled *lymphatics;* these form distinct plexuses in the vascular and nervous layers, whilst a few may be distinguished in close proximity to the muscular tunic of the vas deferens.

Besides the above-mentioned structures, the body known under the names of *Parepididymis,* or the organ of Giraldés, composed of tubes, is found at the commencement of the spermatic cord. The tubes are lined by columnar epithelium, differing in no respect from that of the vas deferens. The subjacent mucous membrane is looser and much folded, the folds in some parts resembling glandular depressions. It is composed of connective tissue and elastic fibres united into a plexus, and of numerous small circularly arranged fasciculi of smooth muscular fibres.

The mucous membrane is surrounded externally by a moderately close venous plexus.

The vas deferens is present in all Mammals, Birds, scaly Reptiles, and Selachii, and invariably possesses distinctly muscular walls. According to Leydig, the vas deferens of Mammals exhibits numerous glands in its lowest dilated portion, the ampulla, whilst that of Birds, Saurians, and Serpents is destitute of glands. The depressions of the mucous membrane, similar to those already described in Man, were doubtless regarded as glands in the above-mentioned animals. The duct common to the urine and semen in Batrachians contains also smooth muscular fibres in its lowest part (Leydig).

II. VESICULÆ SEMINALES.—In the vesiculæ seminales the same parts are found with a few modifications that have just been seen to be present in the vas deferens. The mucous membrane forms numerous folds of unequal height, that have not always a longitudinal disposition, but in some parts form transverse ridges, and thus the depressions are produced that were considered by Henle to be glands; the epithelium, like that of the vas deferens, is columnar, and the individual conical or columnar cells are provided with a well-marked basal border of rods that, especially in newly born children, closely resemble short fine cilia.

The thickness of the mucous membrane amounts to 0·04 of a

millimeter, and into all parts of its substance, and even into its folds, a few isolated small muscular fasciculi penetrate.

The muscular tunic consists chiefly of three layers—an internal longitudinal, a middle circular, and an external, which is again longitudinal. The internal is the strongest; the middle and external are of about equal thickness. In the new-born child the thickness of the internal and middle layers amounts to 0·12 of a millimeter, that of the external to 0·03 of a millimeter. External to the muscular coat is a tunica adventitia containing numerous vessels and nerves. The

Fig. 212.

Fig. 212. Transverse section through the wall of a vesicula seminalis from a Child. *a*, Epithelium ; *b*, mucous layer ; *c*, internal ; *d*, middle ; *e*, external muscular layer ; *f*, tunica adventitia ; *g*, ganglia. Magnified with Hartnack's objective system No. 4, ocular 3.

ganglionic nodules of the nervous plexus attain their greatest development in the vesiculæ seminales, where, in addition to numerous large uni-nucleated ganglion cells, they exhibit others that are bi-nucleated. The seminal vesicles of Mammals, according to Leydig, are glandular organs, and in accordance with this either consist of closely approximated acinous glands, or are constructed on the type of a solitary acinous gland.

III. Ductus Ejaculatorii. — These are lined at their commencement by a single layer of columnar epithelium, the cells, of which are 0·014 of a millimeter in height. The

epithelium of the ducts, as it approximates the vesicula prostatica, quickly begins to assume the transitional form, presenting a superficial layer of short cylindrical or club-shaped cells, and a deep one of smaller almost polyhedric or but little elongated cells. At the openings of the ducts the laminated pavement epithelium of the vesicula prostatica is continued for a short distance into their interior. The surface of the mucous membrane is here also irregular, presenting longitudinal and transverse rugæ, which increase in number and size towards the opening of the ducts. The mucous membrane is 0·06 of a millimeter in thickness, and is composed of connective tissue arranged in the form of a plexus, the fibres of which for the most part run parallel to the axis of the tube, and are accompanied by some longitudinal fasciculi of smooth muscular tissue. Outside the mucous membrane is a circular layer of muscular tissue, having a thickness of 0·66 of a millimeter which is prolonged beyond the ductus ejaculatorii into the circular muscular layer of the vesicula prostatica to be presently described.

IV. PROSTATE.—The structure of the prostate presents two distinct constituents—gland substance and muscular tissue. The latter, as Kölliker has shown, constitutes the proper stroma of the prostate, whilst the connective tissue only forms very thin trabeculæ, representing the septa of the muscles and the supporting material for the vessels and nerves that penetrate from without into the substance of the organ. The prostate is invested externally by a sheath of connective tissue that is directly continuous with the tendons of the smooth muscular bands in immediate contact with it. These last run either circularly or obliquely, with a few longitudinal fasciculi interspersed amongst them, and collectively form the proper cortical substance of the prostate. From the cortical muscular layer strong bands of smooth muscular fibres run towards the centre, decussating freely in their course, and forming meshes in which the gland substance is imbedded. The thickness of the muscular cortex is different in that portion of the organ which is in front of the urethra from that which lies behind it; and in the latter again it differs in its upper, middle, and lower parts;

so that whilst the portion anterior to the urethra consists exclusively of cortical substance, that is to say, chiefly of muscular tissue, the posterior periphery of the prostate has the cortex of the upper segment thicker than that of the middle, and this again thicker than that of the lower portion. It may also be perceived that the gland substance is most strongly marked in the lower portion of the prostate lying behind the urethra, whilst it is sparing in quantity in the parts lying in front of the latter. The arrangement of the gland substance is intimately connected with the muscular bands penetrating it. In the lower segment of the prostate lying behind the urethra, the muscular bands form a loose wide-meshed structure, giving to this potion of the gland a spongy character. In the middle segment they form a regular tunic, investing the central uniformly dense hemispherical gland mass, and from this tunic delicate fasciculi are given off that dip inwards between the gland lobules of the central mass. Lastly, over the upper segment the muscular bands are quite unequally and irregularly distributed. Thus it comes to pass that in the portions of the prostate lying behind the urethra we have an upper more compact segment of the gland substance, a middle homogeneous segment, having a diameter in the adult of 6·6 millimeters, and an inferior portion of more spongy texture.

In structure the gland presents the characters of the so-called acinous glands, in which a gland duct bounded by a structureless membrane divides, after pursuing a slightly sinuous course, into two or more tubes provided with lateral and terminal dilatations of various size and spherical or ovoid shape. The wall, however, always remains structureless.

In the central glandular mass the secondary ducts opening into the principal excretory duct are beset with hemispherical projections—acini. In the lower segment only highly tortuous ducts are present, which undergo frequent subdivision, exhibit numerous dilatations of considerable size, and are singularly looped and coiled at their extremities.

The epithelium lining the acini and ducts is chiefly disposed in a single layer of columnar form, the cells having a height of 0·026 of a millimeter; at certain points, however, as, for

example, in the lower spongy glandular mass, the epithelium is shorter and cubical, and there is a subjacent layer of smaller rounded cells.

The individual cells are cylindrical or conical, with a spheroidal nucleus that is almost invariably situated in the external third of the cell. In the smaller excretory ducts there is here and there a second layer of small rounded cells, containing a relatively large nucleus lying beneath the upper tier; fusiform cells also occur between the outer extremities of the cells forming the moist superficial layer. It is in these fusiform cells that a direct connection of the cell process with the adjoining tissues can be more particularly observed.

As the excretory ducts approximate their orifices they become narrower, and their columnar epithelium more and more modified. In the excretory ducts of the central glandular mass having a diameter of 0·31 of a millimeter, which almost exclusively open at the base of the colliculus seminalis, the transitional epithelium of the urethra is continued for some distance; and sometimes the epithelium of the excretory ducts, as far as to the orifices of those having a diameter of 0·13 of a millimeter, or even at certain points in the vicinity of these openings, is distinctly tesselated and laminated. The excretory ducts of the very small portion of the prostate situated in front of the urethra, as well as those of the upper and lower segments of the portion lying behind it, which for the most part open through the lateral wall of the urethra, are lined near their orifice with laminated tesselated epithelium, and not unfrequently with laminated transitional epithelium.

Transversely striated muscular tissue also occurs in the prostate in the form of continuous bands, internal to the transversely striated fibres of the sphincter urethræ. Henle described similar circular bands existing in the uppermost of those portions of the prostate lying in front of the urethra; they extend, however, as Kölliker has shown, further downwards in the cortical portion of this segment. Fasciculi of transversely striated muscular fibres are found also in the cortical layer of the segment situated behind the urethra, especially in the upper part, where, in company with trabeculæ of smooth muscular tissue, they penetrate into and divide the

gland substance. The vessels and nerves form a dense plexus in the loose and fatty connective tissue of the tunica adventitia, especially in the posterior parts of the prostate.

Fig. 213.

Fig. 213. Transverse section through the colliculus seminalis of a Child. *a*, Superficial epithelium ; *b*, vesicula prostatica ; *c*, its epithelial lining ; *d*, muscles ; *e e*, ejaculatory ducts ; *f*, excretory ducts of the prostate gland ; *g*, upper wall of the urethra ; *h*, vertical muscles. As seen with Hartnack's objective system No. 2, ocular 3.

From the vessels ramifying on the surface of the prostate, large trunks penetrate into the interior, and form a wide-meshed capillary system around the gland. Large arterial vessels run

through the colliculus seminalis as far nearly as to the urethra, where they break up into capillaries. The veins originating in these capillaries join the veins of the urethra. The *nerves* appear as medullated fibres distributed through the cortical portion of the prostate, they here also contain numerous large ganglion cells, or communicate with oval ganglionic swellings. The latter are less numerous than in the vesiculæ seminales, and their diameter is about 0·53 of a millimeter. On the side of the prostate J. Müller observed there were already ganglia on the lymphatic nerves.

Fig. 214 A.

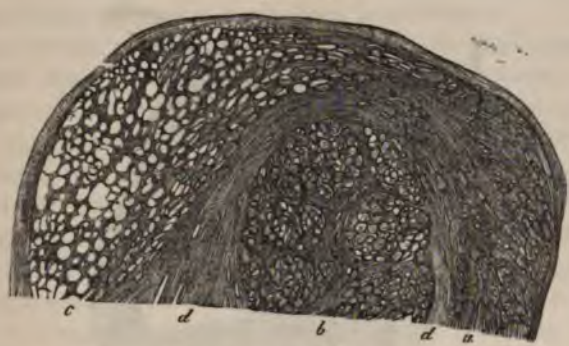

Fig. 214 A. Longitudinal section of the segment of the prostate that is situated behind the urethra of an adult. *a*, Compact; *b*, central; *c*, spongy glandular substance; *d*, muscular investment of the central portion. Magnified three diameters.

Pacinian bodies are also found in the cortex of the prostate. The substance of the organ is traversed by very numerous small fasciculi of medullated fibres that everywhere form plexuses, and numerous nerve trunks run vertically between the sphincter urethræ and the circular transversely striated muscular fibres of the cortical portion, where they ascend to the urethra. Interspersed amongst their fibres are chains of ganglion cells.

In many of the ducts and acini yellowish or brownish scaly masses are found, which are to be regarded as a secretion of the glandular epithelium, and their formation can be followed here in precisely the

same mode as in the thyroid gland. Such yellow and brown pigment scales, and fusiform cells containing pigment granules, may be found both in the cortex and in the gland substance.

A peculiar organ exists in the upper and posterior segment of the prostate, presenting the aspect of a large duct, the wall of which resembles that of an artery, being composed of an internal longitudinal, a middle circular, and an external longitudinal layer. The middle layer consists chiefly of smooth muscular fibres, whilst these are less numerous in the internal and external layers. The interior of this structure is filled with numerous small vascular plexuses, pigmentary concretions, and trabeculæ of smooth muscular fibres.

Fig. 214 B.

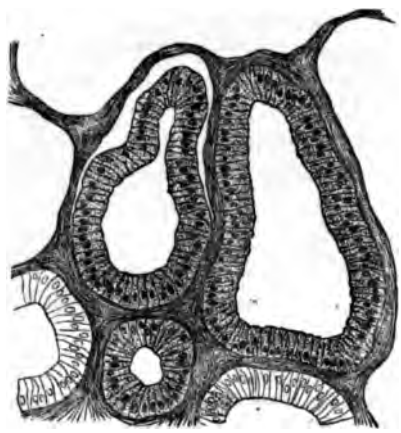

Fig. 214 B. Section through the central gland substance of the prostate of an adult, as seen with Hartnack's objective system No. 5, ocular 3.

The prostate is always present in Mammals, but there is no analogous organ in Birds. In the urodelous Batrachia, the pelvic and anal glands, that swell up during the procreative season, and discharge their secretion into the cloaca, may perhaps correspond to the prostate and the glands of Cowper. Similar organs open into the cloaca of Saurians. In Fishes there are aggregations of acini that communicate with the vas deferens by means of ducts (Leydig).

V. COLLICULUS SEMINALIS.—The colliculus seminalis is invested by a beautifully laminated pavement epithelium. This

is also the character of the epithelium of the lower wall of the urethra. The thickness of this layer is considerably greater at the base than at the apex of the colliculus. In the former situation it amounts to 0·31 of a millimeter, but in the latter it does not exceed a third of this thickness. At the base large conical papillæ, somewhat dilated at their extremities, and containing vessels, project into the epithelium, but towards the apex they become progressively smaller, till at the apex itself they are no longer perceptible. The vesicula prostatica is also lined by a laminated pavement epithelium into which small conical papillæ project. Both upon the colliculus and in the vesicula, short-branched and tortuous glands open, into which the laminated pavement epithelium is prolonged.

The vesicula prostatica is surrounded by a small quantity of vascular connective tissue, and by numerous muscular fibres. The latter are in direct connection with the smooth muscular fibres that extend upwards from the deeper portion of the prostate, as well as with those that are found in the wall of the ductus ejaculatorii. In general it may be said that the fasciculi in immediate contiguity to the vesicula prostatica decussate obliquely with one another. To these oblique fibres there succeeds a circular layer, which may be regarded as the direct prolongation of the external circular muscular layer of the ductus ejaculatorii. This circular layer investing the vesicula prostatica is most feebly developed in the neighbourhood of the epithelium of the colliculus seminalis.

VI. URETHRA.—The epithelium of the urethra, along the lower wall of the root of the pars prostatica and membranacea, is a laminated pavement epithelium; at the sides and upon the upper wall of these parts it is in great part a laminated transitional epithelium, in which are a few small islands of laminated pavement epithelium.

This transitional epithelium, however, is so far peculiar that the middle cells are clavate, whilst the upper are partly tesselated and partly clavate. The thickness of the epithelium varies from 0·09 to 0·1 of a millimeter, and it is somewhat thinner on the upper wall than upon the lower.

The mucous membrane has an average thickness of 0·36 to

0·45 of a millimeter, and is inversely proportional to the succeeding muscular tunic. Its structure, however, differs somewhat in the child from that of the adult.

In the child, both the mucous membrane and the septa of the muscular tunic connected with it consist of a very delicate homogeneous network, in the nodal points of which, at many points in the newly born child, distinct cells containing nuclei may be found connected with one another by short thick processes, and everywhere also in connection with the tunica adventitia of both the larger and smaller vessels. Trabeculæ composed of a fasciculus of delicate connective-tissue fibrils, are moreover visible in this plexus, rendering it not improbable that fasciculi of connective tissue proceed from the fibrillation of the cell processes of this adenoid plexus. In point of fact, in the adult, meshes of decussating fasciculi of connective tissue occur, together with plexuses of elastic fibres.

Numerous small conical papillæ, which are smaller and fewer in number in the upper and lateral walls than in the lower, project from the surface of the mucous membrane into the deep surface of the epithelium.

Glands also occur in the mucous membrane, in the form of branched tubes, presenting two or more dilatations, and bounded by a structureless wall. The dilatations and the portion of the tubes situated in the deeper part of the mucous membrane are lined by a single layer of beautiful columnar epithelium, which nearer the orifice changes into laminated transitional epithelium, and at the orifice itself becomes laminated and tesselated.

These glands—Littré's glands of the urethra—are found both in the lower and lateral wall of the pars prostatica, and in the pars membranacea, where they are scattered over the whole periphery, penetrating to various depths into the mucous membrane, and, indeed, in part dipping between the vessels of the great venous plexus, where they are invested by unstriated muscular tissue, whilst they in part extend to the muscular tunic.

The muscular tunic at the root of the urethra is arranged in two layers, an internal circular and an external longitudinal layer, both composed of smooth muscular fibres.

In the lower wall the circular layer consists only of small fasciculi, separated from each other by a considerable quantity of connective tissue, and in the child has a thickness varying from 1·3 to 1·6 of a millimeter. The external layer is somewhat thinner, being composed of smaller fasciculi. The two layers are connected with one another by oblique and decussating fasciculi.

Towards the upper wall of this portion of the urethra the two layers become somewhat more continuous, the fasciculi of each being larger and more closely approximated. Throughout the whole periphery of the tube, however, small fasciculi enter the mucous layer obliquely, and break up into isolated fibres which may be followed to the epithelium.

In the pars prostatica the musculature of the urethra is intimately connected with that of the prostate, the fasciculi of which, composed of unstriated fibres, are recognizable, running for the most part longitudinally immediately beneath the mucous membrane.

In the pars membranacea a continuous layer of longitudinal muscular fibres, having a thickness of 0·58 of a millimeter, is alone distinguishable immediately beneath the mucous membrane, and from this numerous fasciculi are given off obliquely, which enter the mucous membrane. The large vascular and nervous trunks lie on the outer side of the muscular tunic, and the arteries, after having distributed numerous branches to this tunic, enter the mucous membrane, where they give off single and double capillary loops to the papillæ, and are then continuous with the subepithelial venous rootlets. These, rapidly increasing in size, and intercommunicating by numerous anastomoses, form a venous plexus belonging to the mucous membrane, the meshes of which have a predominating longitudinal direction.

Between these large veins muscular bands from the muscular tunic extend into the mucous membrane. The thickness of this venous plexus gradually increases towards the anterior extremity of the pars membranacea.

In their course outwards these veins decrease again in number and size, or, in other words, from this venous plexus smaller veins run outwards, which receive, as they perforate it, the veins of the muscular tunic.

From this description it is obvious that on the occurrence of an increased flow of blood through the arteries of this portion of the urethra, the discharge of such blood through the corresponding veins cannot take place with the same rapidity, and hence an accumulation of any surplus supply must occur in the large venous plexuses of the mucous membrane. Hence it follows that these plexuses constitute an erectile tissue, and that, in accordance with Henle, we may regard this portion of the urethra as, though undoubtedly only feebly developed, an erectile body.

The nerves here exhibit relations similar to those that have been already described; ganglionic nodal points being distributed in the trunks, which are composed of medullated fibres, that run externally to the muscular coat.

Lovén has described ganglion cells and ganglion nodes as existing (1) in the posterior surface of the pars membranacea urethræ; (2) in the dense connective tissue on the posterior part of the bulb; and (3) in the plexuses formed around the vessels by the lateral fasciculi of the nervi erigentes at the side of the bulb.

Before the corpus cavernosum urethræ enlarges to form the bulb, and where the crura penis are already in close proximity to the urethra, but are still below it, a longitudinal mass of smooth muscular fibres penetrates between the two ischiocavernosi and the perinæal muscles, consisting of variously sized fasciculi, and having a circular area of about 2·25 millimeters in diameter. The fasciculi of which it is composed are more closely compressed towards the centre of the mass than at the circumference. Those near the upper portion of the periphery which is turned towards the urethra are oblique or even almost circular in direction. With it a continuous layer of longitudinal fasciculi of smooth muscle lying between Cowper's glands and their excretory ducts, that is to say, the crura penis, is directly connected. This mass of muscle is separated from the excretory ducts of Cowper's glands only by a layer of smooth muscular fibres that run parallel to the ducts. The thickness of this muscular layer between the glands of Cowper amounts to 0·89 of a millimeter, and between the crura penis to 0·54 of a millimeter.

Numerous fasciculi are given off from this muscular mass,

which penetrate between the lobules of Cowper's glands, where they break up and become associated with transversely striated muscles (ischio-cavernosi and perineales) entering the substance of the gland from below and externally.

The above-mentioned muscular layer is also connected with the muscular trabeculæ of the crura penis.

Superiorly this muscular layer, becoming pointed like a gable end, and diminishing in breadth, is continuous with a septum of connective tissue, which is again itself continuous with the fasciculi of connective tissue lying on the under surface of the corpus cavernosum urethræ (corpus spongiosum). Applied to this septum at an obtuse angle on either side, is a longitudinal layer of muscular fibres 0·54 of a millimeter in thickness, which is a direct continuation of the muscular tissue of the urethra, and surrounds whilst it is also continuous with the muscular trabeculæ traversing the substance of the corpus cavernosum urethræ. Where the muscular layer is in apposition on either side with the above-mentioned septum, several large veins exist, arising vertically from the erectile tissue of the crus penis (corpus cavernosum), and penetrating into the erectile tissue of the urethra (corpus spongiosum).

We may here appropriately consider the glands of Cowper. Their position has already been indicated, and it only remains to describe their structure.

Cowper's glands are of oblong form, with their long diameter directed downwards and inwards. Each possesses a duct lined by columnar epithelium, and having a diameter of 0·18 of a millimeter, which ascends by the side of the crus penis, and, as has been already mentioned, is accompanied by a layer of smooth muscles running parallel to its longitudinal axis. As the ducts approximate the urethra, they diminish in diameter. Each duct subdivides several times, and the branches have two or more terminal dilatations of 0·08 to 0·12 of a millimeter in width, which constitute acini. The structureless walls of the acini are lined by columnar epithelium.

The gland substance is here, as elsewhere, surrounded by a tolerably close plexus of capillaries.

The fibrous material in which the gland substance is imbedded is partially composed of connective tissue, but chiefly

of those muscular fibres to which reference has already been made.

Near the bulb the whole of the lower and a great part of the lateral portion of the urethral mucous membrane is lined by a laminated pavement epithelium 0·18 of a millimeter in thickness. This layer resembles that of the oral cavity and of other parts, except that the uppermost cells do not appear to be so strongly flattened, whilst some contain an oblong and others a more rounded nucleus. The cells of the deepest layers are rounded or polyhedric, with spheroidal and relatively large nuclei. Proceeding from the bulb, the surface lined by this laminated pavement epithelium gradually diminishes in extent, being found only for a short distance along the median line of the lower surface of the urethra, where it is replaced at first by laminated transitional and subsequently by columnar epithelium. This replacement occurs earlier at the sides, and still sooner on the upper surface.

Variations, however, occur in this respect; islands of laminated pavement epithelium not unfrequently occurring in newly born children, both on the upper and lower surfaces of the urethra, in the body of the penis. The columnar epithelium with which the urethra is lined to near the fossa navicularis presents columnar cells in the most superficial tiers, whilst those composing the middle and deeper layers are clavate or fusiform. At certain points there is only a single layer of columnar cells. As the lumen of the urethra begins to be elongated vertically from above downwards, its whole surface is invested with laminated pavement epithelium, which however forms a much thicker layer on the lower than upon the upper surface. The epithelium of the upper half is further distinguished from that of the lower by its superficial cells being more flattened and coalesced with one another. The deepest layer of the epithelium, both on the upper and lower part, consists of short columnar cells with rounded nuclei, arranged in a palisade-like manner.

The mucous membrane of the urethra everywhere presents longitudinal folds, which are joined at certain points by transverse membranous processes forming the lacunæ of Morgagni.

The thickness of the mucous membrane varies considerably

at different points, since its external boundary cannot be exactly determined; its vessels and muscles being gradually continuous with those of the corpus cavernosum. At the root of the penis its thickness is about 0·178 of a millimeter, but more anteriorly it is thinner, not exceeding 0·13 of a millimeter.

Fig. 215.

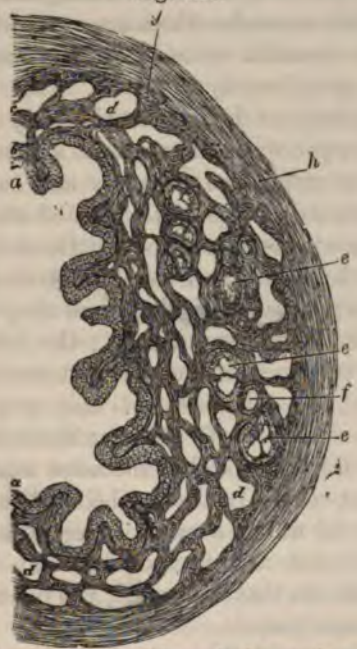

Fig. 215. Transverse section through the urethra (pars cavernosa) of a Child. *a*, epithelium; *b*, mucosa; *c*, muscular trabeculæ; *d*, blood cavities of the corpus cavernosum; *e*, glands; *f*, excretory duct of the glands; *g*, longitudinal muscles; *h*, albuginea. As seen with Hartnack's objective system No. 2, ocular 3.

The papillæ of the mucous membrane which project into the deep surface of the epithelium are only numerous and strongly developed where the latter is laminated and tesselated. Where it is of the transitional form, the papillæ are short, and few in number. They attain their greatest length on the lower wall of the fossa navicularis and towards the orificium urethræ, where they are as long as 0·14 of a millimeter. All the papillæ

of the urethra are vascular, and possess a single or, as in those of the fossa navicularis, several capillary loops. When the papillæ are absent, as in those parts invested by columnar epithelium, there is a close subepithelial capillary plexus distributed immediately beneath the surface. The mucous membrane is looser, and consists of a delicate meshwork of connective tissue, in which small isolated longitudinal and oblique fasciculi of smooth muscular fibres are everywhere found, that proceed from the muscular trabeculæ of the corpus cavernosum urethræ (corpus spongiosum).

The mucous glands of Littre are tolerably abundant, especially upon the upper wall. They form sinuous canals, perforating the mucous membrane obliquely, and having a diameter of 0·13 of a millimeter. The epithelium of the surface of the mucous membrane is continued for a little distance into their interior. These tubes are undivided until they enter the substance of the corpus cavernosum, where they present four or five hemispherical dilatations or acini; the latter have a diameter of 0·08 to 0·12 of a millimeter, and are not unfrequently in contact with the albuginea of the corpus cavernosum urethræ (corpus spongiosum). The epithelium of the greater part of the excretory duct and of the acini consists of a single layer of columnar cells. In the epithelial cells of the acini, the nucleus, even in the newly born child, is by no means everywhere spheroidal, but is flattened as in adults, with its long axis at right angles to that of the cell, and in immediate contact with the membrana propria.

As the greater part of these glands everywhere lie between the vessels of the corpus cavernosum, and are consequently surrounded by muscles, it is quite obvious that the erection of the organ must exert a considerable influence on the discharge of their secretion, whilst it may also influence its production.

The lymphatics of the urethra are moderately numerous; they lie in the mucous membrane near the epithelium, run parallel to the long axis of the canal, and communicate freely by means of transverse and oblique anastomosing branches. They attain their greatest development on the lower wall of the fossa navicularis.

VII. PENIS.—The albuginea of the corpus cavernosum urethræ, and that of the corpora cavernosa penis, is composed of connective tissue, elastic fibres, and partially of muscular fibres. The former consists of slightly wavy parallel fasciculi of fibres like those of tendinous tissue.

These fasciculi of connective tissue form a circular layer around the corpus cavernosum urethræ, that is continuous externally with the loose subcutaneous connective tissue. In the erectile bodies of the penis the fasciculi are arranged in two layers, an external longitudinal and an internal circular, though the former only occurs on the upper and lateral periphery of each corpus cavernosum, whilst the circular layer is continued to the lower surface, and forms a septum in the median line between the two corpora cavernosa.

In the newly born child, the thickness of the external longitudinal layer at the root of the penis is 0·31 of a millimeter; that of the internal, 0·49 of a millimeter. In the shaft of the organ this proportion is inverted; the thickness of the external layer being here 0·45 of a millimeter; that of the internal, 0·26 of a millimeter. Numerous fusiform cells are distributed amongst the fasciculi of the connective tissue.

The elastic tissue both in the albuginea of the corpora cavernosa penis and in that of the urethra, forms dense plexuses of delicate fibres, containing oblong nuclei in the new-born child. Another kind of plexus, more or less close and of variable extent, composed of the nucleated cells very similar to those of embryonic tendinous tissue, is also present in the albuginea of the corpora cavernosa, as well as in the loose surrounding tissue.

Smooth muscular fibres occur, especially in the body of the penis, both in the corpus spongiosum urethræ and in the corpora cavernosa penis. They are most numerous in the former, in which they pursue a circular course, whilst in the latter they are circular in the circular layer, longitudinal in the longitudinal, and where the albuginea consists of only a single layer, exclusively circular.

Large nerve trunks, composed of medullated fibres, run in the loose tissue in immediate contact with the albuginea. In the new-born child many of them lie with small bloodvessels close to the albuginea, in oblong spaces filled with lymph

corpuscles, and surrounded by connective tissue, which may be regarded as belonging to the lymphatic system.

From the nerve trunks lying external to the albuginea smaller branches extend into the corpora cavernosa, where they first appear as medullated, and in their further course as non-medullated, fibres. They proceed from the plexus cavernosus of the sympathetic, and to a smaller extent from the nervi pudendi, the greater portion of the fibres of which are distributed to the skin and the mucous membrane of the urethra.

Groups of fat cells and Pacinian corpuscles are distributed in the loose tissue surrounding the albuginea. The latter occur alike in the root and shaft of the penis, and in the vicinity of the corona glandis. They have been seen by Schweigger-Seidel at a distance of from eight to ten millimeters behind the posterior border of the glans. They all present an elliptical form, with their long axes arranged parallel to that of the penis. Their axis-cylinders are very broad, and do not divide at the apex of the corpuscles. I have myself observed them in the corpus cavernosum of the crus penis.

In the corpus cavernosum penis the muscular fasciculi are collected into a longitudinal layer of 0·09 of a millimeter in thickness, lying externally to the albuginea, which is continuous by means of oblique fasciculi with the muscular bundles of the corpus cavernosum lying internal to the albuginea. This external muscular layer is only partially and feebly developed on the corpus cavernosum urethræ, and is therefore to be regarded as a special layer belonging to the corpus cavernosum penis, and especially developed on its dorsum and sides. The muscular trabeculæ stretched between the vascular spaces, and bounding the latter, consist partly of longitudinal, partly of oblique, and partly of circular fasciculi, which consequently decussate in various directions.

The individual muscular fibres are very short in proportion to the length of their nuclei.

The bloodvessels of the corpora cavernosa are arteries, capillaries, veins, and a close plexus of spaces bounded by muscular fasciculi, and lined by tesselated epithelium—the corpus cavernosum, in the proper sense of the word.

The corpus cavernosum urethræ is more strongly developed upon the lower than upon the upper segment. The large cavernous spaces extend in the latter up to the tunica albuginea, whilst in the lower, and partly also in the lateral portion, an almost continuous muscular layer lies between a kind of cortical vascular layer and the principal mass of the corpus cavernosum, which is only interrupted by a few vessels proceeding from the cortical layer to the interior. A similar arrangement occurs in the corpus cavernosum penis; the largest spaces are in the centre; from thence towards the periphery in each half they rapidly diminish in size, becoming gradually replaced by a layer consisting almost entirely of muscular fibres, whilst still more externally they form a cortical layer in immediate contact with the albuginea.

The cavities diminish but little in size from the centre of each corpus cavernosum towards the septum. Those of each corpus lying close to the septum communicate with one another by oblique and transverse anastomoses, which are accompanied by corresponding transverse connecting trabeculæ of muscular fibres.

Proceeding from the corona glandis towards the anterior extremity of the penis, the corpus cavernosum urethræ gradually diminishes in thickness, attenuating first upon the upper and then upon the lower wall. A few transverse branches still exist on the upper part, that establish a communication between the vascular cavities of the two sides; in the lower part a connective-tissue septum, corresponding to the frænulum præputii, penetrates its substance, so that anteriorly the corpus cavernosum urethræ appears to be divided from below into two segments. Such connective-tissue structures sometimes, like a complete tunica albuginea, divide off an elliptical area within the corpus cavernosum urethræ, so that a small corpus cavernosum appears to be present on each side within the corpus cavernosum urethræ. Just as the corpora cavernosa penis terminate with conically pointed extremities in the glans, the corpus cavernosum urethræ begins also to lose its individuality, and becomes completely fused with the corpus cavernosum of the glans. This presents a fissure below, and in the vicinity of the orificium urethræ it is divided by the entrance

of a connective-tissue septum from above into two halves, which, however, still remain partially united by transverse anastomoses. The want of continuity of the corpus cavernosum glandis upon the lower wall is occasioned by fasciculi of connective tissue, which project upwards from the tissue surrounding the urethra.

The trabeculæ between the vessels in the glans contain fewer muscular fibres than those of the corpus cavernosum penis and urethræ.

In the lower and external portion of the corpus cavernosum glandis are the largest vascular spaces in close juxta-position, whilst in the upper parts they diminish in number and size. A fine vascular plexus is stretched between, and communicates with them, which will be subsequently more fully described, and a similar plexus is strongly developed in the lower and lateral portions.

The vessels that run in the prepuce are directly continuous with the cortex of the lower split segment of the glans.

As regards the arteries of the organ, it is well known they are branches of the arteria pudenda communis; and, indeed, according to Kobelt, they are the arteria bulbina, bulbo-urethralis, dorsalis and profunda penis.

From the latter the arteria bulbosa penis runs to the root of the penis, forming anastomoses with its fellow of the opposite side, and from these arches the arteria cavernosa penis proceeds to the corpus cavernosum penis, and extends to its extremity.

The arteria dorsalis penis is principally distributed to the glans, but partly also to the corpus cavernosum penis.

According to Jarjavay and Sappey, from five to eight branches arise from the dorsalis, and wind around the penis, anastomosing with the bulbo-urethralis, and ultimately supplying the corpus cavernosum urethræ. According to Langer, there are four or five pairs of rami perforantes distributed to this part, which anastomose both with the branches of the dorsal artery as well as with the arteria bulbo-urethralis. The same observer admits, in addition to these rami perforantes of the arteria cavernosa penis, other arteriæ septi, which, arising from the arteria cavernosa penis, ascend close to the septum towards the vena dorsalis penis, anastomose with one another, and, as

accessory branches to those of the dorsalis penis, with which they anastomose, also supply the albuginea of the corpora cavernosa penis.

Johann Müller, as is well known, divided the arteries of the corpus cavernosum into rami nutritii and arteriæ helicinæ, the former constituting the arteries of the trabecular tissue—vasa vasorum—which, after frequent anastomoses amongst themselves, break up into capillaries. The arteriæ helicinæ he described as branches having a length of one line, and a diameter of one-fifth of a millimeter, which, both separately and in whorls, project with their horn-like swollen extremities into the cavernous spaces, where they terminate cæcally. When erection commences, he conceived that these extremities open, and thus the cavernous spaces become filled with arterial blood.

Whilst some inquirers, as Krause, Valentin, Kobelt, Kölliker, Hyrtl, Gerlach, and Henle, have adopted these views, and others, as Valentin, M. J. Weber, Arnold, Segond, Kohlrausch, Kölliker, Henle, and Rouget, have contested their truth, Langer has recently, by his comprehensive and perfectly correct statements, shown them to be really inaccurate.

He, with Valentin, Arnold, and Henle, has shown that the greater number of the arteriæ helicinæ are only one limb of a more or less completely injected arterial loop, and that the occurrence of the arteriæ helicinæ is dependent upon the form of the muscular trabeculæ, since the arterial twigs run straight in the cylindrical or funnel-shaped convoluted laminæ of the shaft of the penis, whilst they form arteriæ helicinæ in the cord-like trabeculæ occurring in this part of the organ. We must therefore agree with Langer in considering all the branches of the arteriæ corporis cavernosi to present characters that are essentially similar. In regard to the mode in which the circulation is completed in the corpus cavernosum penis, Johann Müller and Krause agree in stating that the arterial blood passes directly from the arteriæ helicinæ into the cavernous spaces. According to Valentin, however, the smallest arteries open by funnel-shaped enlargements into the venous spaces, whilst according to Rouget, these spaces are continuous with the arteries of the trabeculæ, after they have formed split-like openings at the surface of the trabeculæ.

Langer has shown that the circulation in the corpus cavernosum penis varies in its ultimate distribution in the cortex and in the middle parts. In the cortex small, but not capillary arterial branches, visible only with a lens, penetrate the coarser cortical layer; but besides these, in the periphery, the blood traverses true capillaries, especially those of the finer capillary plexus here present. In the interior of the erectile body the blood likewise flows through capillaries.

The entire periphery of the erectile body is the principal atrium through which the arterial blood gains access to the erectile plexus.

Moreover, in the interior of the erectile body there are direct anastomoses between the arteries and the larger veins, and this is effected by conical rootlets which form a constituent part of the internal convolute of veins.

Thus there are three modes in which the blood passes from the arteries into the veins in the corpus cavernosum penis; namely, (1) through direct anastomoses between the larger arterial and venous branches; (2) through the coarser cortical plexus which receives the finest arterial branches; and (3) immediately through capillary vessels, as in the finer cortical plexus, and in the interior of the corpora cavernosa. The erectile plexus of the penis is a true venous plexus.

The veins that emerge from the corpora cavernosa penis are the dorsal veins which open into the vena dorsalis, and constitute the venæ emissariæ of Müller, and the veins of the inferior surface of the penis, which are the venæ emissariæ of Kohlrausch.

The former arise directly from the cavernous plexus, the latter from the interior of the corpora cavernosa, and pass through spaces of the cortical plexus. This relation is of great importance for the production of erection, since by the filling of the cortical plexus, which, as above mentioned, is the chief atrium compression of the efferent veins must necessarily be produced.

In the crura penis the efferent venous channels form the venæ profundæ. These, as Langer has shown, are by no means direct continuations of the large erectile veins, but arise from them by smaller rootlets.

The erectile plexus of the corpora cavernosa penis is on this account, according to Langer, to be regarded as "a spacious rete mirabile, which, in regard to the vena dorsalis, is unipolar; but in regard to the venæ profundæ, is bipolar."

The same author distinguishes an external and an internal part in the corpus cavernosum urethræ. The external consists of a dense plexus of veins, forming the rete mirabile venosum of Kohlrausch and Jarjavay, and constituting the proper erectile body of the urethra. The inner part is the venous plexus of the urethra itself, and is composed of smaller longitudinal and perfectly parallel vessels that communicate by means of numerous short and tortuous anastomoses. The outer part is continued uninterruptedly into the bulb as an erectile plexus, whilst the inner is continued through the pars membranacea and prostatica to the bladder in the form of a submucous venous plexus.

The arteries give off some branches to the mucous membrane of the urethra, where they break up into capillaries, whilst others remain in the corpus cavernosum, and then divide into their capillary branches.

The circulation in the corpus cavernosum urethræ is everywhere accomplished by means of capillaries. The roots of the venous efferent canals—the venæ efferentes—arise from smaller vessels coalescing to form single trunks.

The vascular system of the glans presents similar characters.

The cavernous tissue here also is a rete mirabile venosum, arising from capillaries (Hausmann, Kobelt, Jarjavay). The coarse venous plexus, as we have already stated, is traversed by a close fine plexus; numerous loops from the most superficial capillary plexus ascend into the papilla of the glans, just as from the cavernous spaces of this body. The branches of these loops are characterized by their tortuous course (Langer), and indeed many of them are distinctly coiled.

The connection of the erectile body of the glans with that of the urethra is effected by the venæ efferentes glandis, the finer branches of this convoluted mass of veins lying in the glans, the coarser in the corpus cavernosum urethræ.

This convoluted mass of veins lies on the dorsal surface of

the urethra, and was first observed by Kobelt. It extends also between the corpus cavernosum penis and urethræ, and appears to constitute a separate erectile body, since smooth muscular fibres are also present in its trabeculæ, and it is not unfrequently bounded by a thin tunica albuginea.

The *mucous membrane of the glans* is covered by laminated

Fig. 216.

Fig. 216. Transverse section of the injected glans penis of a newborn Child. *a*, Epithelium of the urethra; *b*, mucosa; *c*, corpus cavernosum urethræ; *d*, corpus cavernosum glandis; *e*, mucous membrane of the glans; *f*, epithelium of the glans. Seen with Hartnack's objective system No. 2, ocular 3.

pavement epithelium, having a thickness of 0·12 to 0·14 of a millimeter, which is distinguished from that of the urethra by its less transparency, and by the circumstance that the cells of the most superficial layer of cells are much flattened

and fused with one another; the nuclei of these cells are all staff-shaped. In the middle layers, well-developed ribbed or spiny cells (Riffzellen) are present, whilst the deepest cells are columnar, and arranged side by side like palisades.

The mucous membrane is rich in elastic plexuses, and presents also closely approximated conical and simple or divided papillæ, that are more distinctly developed in the adult than in the newly born infant.

The nerves of the glans are very numerous, and, according to Kölliker, end within the papillæ in Krause's terminal bulbs.

The prepuce presents the same general character as the skin. The epithelium of the internal lamina, however, resembles laminated pavement epithelium.

In the skin of the penis, as well as in both laminæ of the prepuce, sebaceous follicles are present. In the latter region they are of oval form, and may have a length of 0·6 of a millimeter and a breadth of 0·35 of a millimeter.

They extend as far as to the corona glandis, constituting the glandulæ Tysonianæ, their size and the number of their pullulations progressively diminishing. In the new-born infant they are abundantly and well developed, both upon the internal and the external layer of the prepuce, whilst in some adults it is difficult to establish the fact of their existence. Sebaceous follicles are, as a rule, absent upon the glans penis, though a few of simple form were on one occasion discovered by Schweigger-Seidel at the apex of the glans. In structure the sebaceous follicles of the prepuce are precisely similar to those of other parts of the skin.

In all Mammals the penis is perforated by the urethra; amongst Birds a true penis is only found in the Struthionidæ and in a few Gallinaceous and some Natatory Birds.

Amongst Amphibia, Turtles possess a single, Snakes and Lizards a double intromittent organ.

The penis of Birds and Amphibia is not perforated, but simply presents a groove for the discharge of the semen (Leydig).

Corpora cavernosa are very generally present amongst Mammals. In Birds a cavernous tissue either surrounds the penis, or is found in its interior (Struthio).

Most Amphibia possess erectile tissue, which either surrounds the penis like a sheath, as in Saurians, or is everywhere well developed in the penis and the glans, as in Tortoises and Crocodiles.

In many Mammals bony plates or rods occur in the penis. Thus, for example, in Cats there is a short osseous lamina at the apex of the glans above the urethra, which posteriorly towards the corona glandis has a small roundish cartilaginous nucleus upon it. The corpus cavernosum glandis extends semi-circularly round the osseous plate and the cartilaginous nucleus.

In Cats, instead of the corpora cavernosa penis, there is a cylindrical body containing fat cells, and enclosed by a dense tunica albuginea, subdivided by a framework of connective-tissue trabeculæ. Along the lower side of this body extends a thin layer of large veins which anastomose with one another to form a plexus.

B. Female Organs.

I. Labia pudendi.—In these all the elements of the skin are present. The basis of the labia majora consists of a meshwork of connective-tissue trabeculæ that radiate outwards towards the periphery. In the deeper parts the meshes are looser, representing the subcutaneous tissue, but towards the epidermis they become denser and closer to form the cutis.

In the looser portions, groups of fat cells, large vessels, and nerves are abundant, together with many large sweat glands and hair follicles. The sebaceous follicles are characterized by their size,—0·5 of a millimeter in diameter,—and also by their opening in some instances by free orifices on the surface of the skin.

Parallel and close to the surface tolerably close plexuses of elastic fibres are stretched, containing regularly arranged smooth muscular fibres (Henle). The papillæ, nerves, Pacinian corpuscles, and vessels, are similar to those of other parts of the skin.

Over that part which is covered by the nymphæ the epidermis becomes somewhat more transparent; the uppermost cells are still much fused together, though they continue to exhibit well-marked rodlike nuclei.

The nymphæ are invested by a laminated pavement epithelium, the lowermost cells of which, in the new-born child, in

many instances contain pigment granules around the spheroidal nucleus.

The subjacent mucous membrane presents on its surface conical closely set vascular papillæ, somewhat dilated at their extremities. The membrane itself is destitute of fat, and contains also smooth muscular fibres in the connective-tissue trabeculæ. The framework of the mucous membrane exhibits the same arrangement as that of the labia majora. A strong trabecular framework, arranged in the form of a meshwork, radiates towards the periphery. Sebaceous glands without hairs are distributed over the nymphæ up to their internal surface, but they are of a smaller size—0·2 of a millimeter—than those of the labia majora, and are not discoverable in the newly born child.

The vessels are branches of the arteria labialis posterior, and form simple but tortuous loops in the papillæ. The capillaries form plexuses upon the surface and in the substance of the nymphæ, from which other plexuses of the smaller veins arise, the latter of which appear to be everywhere traversed by the capillary plexuses (Gussenbauer). The nymphæ therefore, like the glans clitoridis, possess an erectile cavernous tissue (Gussenbauer).

II. Clitoris and Vestibulum.—The mucous membrane which, through the præputium and frenulum clitoridis, is directly continuous with the nymphæ and the mucous membrane of the vestibule, is constructed, in regard to its epithelium, mucous tissue, papillæ, and nerves, on exactly the same type as the nymphæ.

On the clitoris the mucous membrane invests the corpora cavernosa and glans clitoridis, which is continuous with the two bulbi vestibuli; the latter correspond to the split corpus cavernosum urethræ of Man.

The corpora cavernosa clitoridis, like the bulbi vestibuli, are enclosed by a fibrous sheath, and are composed of a venous plexus everywhere traversed by numerous smooth muscular fibres. In other respects they resemble the corresponding parts of the male, and here also stand in direct continuity with the vascular loops of the papillæ. Gussenbauer, in his exhaustive

description of the mode of vascular distribution of the external organs of generation in the female, established the following points in regard to the already long-acknowledged analogy of the corpora cavernosa penis and clitoridis:—

1. The small arteries pour their blood towards the root of the clitoris directly into large veins.

2. The finer venous plexus near the surface receives arterial blood through minute arterial branches.

3. The capillary plexus just beneath the surface of the anterior extremity of the organ into which the arteries for the most part break up, forms, by means of the venous plexus with which it is continuous, the transition into the coarse erectile plexus.

The erectile plexus of the bulbus vestibuli has a structure similar to that of the clitoris. The external surface of the bulb is formed by a coarse, the internal by a fine, venous plexus. The latter is traversed by the veins uniting with that venous plexus in the submucous tissue of the urethra and of the vestibule, which is spread over the anterior wall of the vagina as far as to the urinary bladder (Gussenbauer).

The efferent venæ profundæ present the same relations to the cortical layer of the erectile body which are so important for the production of erection, as in the penis. Of equal importance for erection are the relations of the efferent veins to the musculi bulbo- and ischio-cavernosi which by their contraction occasion compression of the efferent veins of the corpora cavernosa clitoridis, and of the bulbus vestibuli.

The pars intermedia is a convoluted mass of veins that emerges from the posterior surface of the clitoris, and constitutes the connection between the corpus cavernosum clitoridis, the bulb, nymphæ, frenulum and glans clitoridis (Gussenbauer).

The mucous membrane of the vestibule presents numerous folds; many glands open upon it, some of which are irregularly distributed over the surface of the vestibulum, whilst others are more closely compressed about the orifice of the urethra and the introitus vaginæ. They appear in the form of branched tubes, with several projections at their deeper part, that are lined throughout by a single layer of columnar

epithelium, except that the laminated epithelium of the surface is prolonged for a short distance into their mouths. The size of the gland varies from 0·5 to 2·5 millimeters.

The *glands of Bartholini* open at the side of the introitus vaginæ, and agree perfectly in structure with the glands of Cowper in the male. They are of an elongated oval form, lie at the posterior border of the diaphragma urogenitale, and stand in intimate relation with the sphincter muscles by which they are more or less surrounded, whilst a few muscular fasciculi also penetrate between the lobules of the gland. This is especially the case in regard to the musculus bulbo-cavernosus. The length of the glands varies from 15 to 20 millimeters; the excretory duct is about the same length, its wall is 0·2 of a millimeter thick, and the tube has a calibre of 1 to 3 millimeters (Henle).

The excretory duct is lined near its orifice by laminated pavement epithelium, but elsewhere the cells are columnar. After undergoing frequent division, it terminates in numerous hemispherical or ovoid dilatations—acini. These acini, like those of the glands of Cowper, are lined by columnar epithelium of variable height.

The bloodvessels of the mucous membrane form superficial plexuses from which loops are given off to the papillæ.

The nerves are composed of medullated fibres proceeding from the sympathetic and pudendal nerves, and are especially numerous in the mucous membrane of the glans. On these nerves the terminal bulbs of Krause and Pacinian corpuscles may be discovered.

III. HYMEN AND VAGINA.—At the entrance of the vagina, the mucous membrane forms a duplicature—the hymen. Its epithelium is laminated and tesselated, and of nearly the same thickness as that of the vestibule—0·3 to 0·5 of a millimeter. The delicate but highly vascular and nervous mucous membrane bristles with close-set, conical, divided, and undivided papillæ, that project into the epithelium, and are from 0·2 to 0·3 of a millimeter long.

The mucous membrane of the vagina is uneven, presenting, especially near the introitus ad vaginam, upon both

the anterior and posterior walls, transverse fold-like or broad papillary and very vascular swellings. These rugæ are partially divided at their free border by furrows of variable depth, and thus form a complex mass of different-sized broad, freely projecting, and club-shaped papillæ.

The vaginal mucous membrane is lined by pavement epithelium of about 0·6 of a millimeter thick, resting on a bed of connective tissue, containing much elastic tissue, from which also papillæ containing vascular loops project into the deep surface of the epithelium.

The submucous tissue is loose, and, as will be presently pointed out, contains numerous vascular meshes.

Subjacent to the mucous membrane, and continuous with it, is the muscular coat, which is arranged in two layers, an internal longitudinal, that is by far the stronger, and an external circular layer. Both also contain oblique decussating fasciculi that pass from one layer into the other.

From the internal layer muscular fasciculi are also given off, which enter the submucous tissue, and from thence pass into the mucosa as far as to the papillæ. These fasciculi are separated from each other by a considerable quantity of connective tissue, so that they do not form a continuous muscular layer.

External to the muscularis is a layer of loose connective tissue, on which the outer venous plexus lies. Towards the fornix all the layers diminish in thickness. The ultimate distribution of bloodvessels in the mucous membrane of the vagina is as follows:—

The arteria vaginalis penetrates into the vagina from behind, but before entering the muscular layer, gives off branches for the anterior and lateral walls. The arterial branches, after they have perforated the muscularis obliquely, break up partly into a submucous capillary plexus, and partly send small twigs into the papillæ, which in those of the upper part form single, but in those of the lower part multiple loops. The capillary loops of the compound papillæ, by their frequent anastomoses, form a plexus from which a vein arises that traverses the axis of the papilla. The rugæ contain numerous large veins that by their anastomoses form a plexus, together with smooth muscular

fibres, which, as has been stated above, proceed from the muscularis. On this account this venous plexus may be regarded as a cavernous tissue (Gussenbauer).

The veins entering the submucosa form meshes elongated in the direction of the long axis of the vagina. They unite to form larger branches, which traverse the muscularis, and constitute the plexus vaginalis. The walls of these vessels present the same trabecular arrangement as is exhibited by other erectile organs.

The vaginal mucous membrane is abundantly supplied with veins and lymphatics, but little is known in regard to their ultimate distribution. Isolated ganglion cells, and groups of the same, are found in the trunks composed of medullated fibres; the latter occur especially in those places where two or more trunks coalesce. The ganglion cells, as has been already noted in the case of the male genitals, are of two different sizes.

IV. URETHRA.—The epithelium lining the upper part of the mucous membrane of the urethra is of a laminated transitional form; the uppermost cells are club-shaped, and form short cylinders; the deeper-seated ones progressively diminish in height, till at length only spheroidal and flattened cells are met with. In the inferior portion, the epithelium resembles that of the vestibule and vagina in being laminated and tesselated; its thickness increases towards the orifice.

Two layers, not very well separated from one another, are distinguishable in the mucous membrane, an internal (mucosa), with numerous papillæ projecting into the epithelium, and an external (submucosa), which contains a cavernous structure composed of a plexus of large veins. The thickness of the mucosa is about 0·13 of a millimeter, whilst that of the submucosa is about five times as much.

The tissue of the mucosa is infiltrated at numerous points with cells resembling lymph corpuscles, and this infiltration is so considerable that the tissue simply consists of a delicate network, the interstices of which are completely filled with cell-like bodies (conglobate gland substance of Henle). In such parts no well-defined limit can be distinguished between the cells of the mucosa and the deepest epithelial cells.

The mucous membrane of the female urethra, like that of the male, exhibits the glands of Littre, which are more abundant near the urethra than in the upper parts.

The muscular coat consists in general of a continuous longitudinal internal layer of unstriated fibres, 1·8 of a millimeter in thickness, and of an external rather stronger circular layer, which is composed internally of smooth and externally of transversely striated fibres (musculus urethralis). The fasciculi of this layer are not nearly so closely applied to one another as are those of the longitudinal muscular layer.

Here and there is an additional longitudinal layer, having a thickness of 0·2 of a millimeter, in which likewise only smooth muscular fibres are to be found. Externally the musculature is invested by a fascia, having a thickness of almost 0·2 of a millimeter, that is composed of parallel, sinuous, and for the most part circular fasciculi of connective tissue. The internal longitudinal muscular layer is not very sharply defined from the submucous tissue, since on the one hand it gives off small longitudinal fasciculi of smooth muscular fibres into the submucous tissue, whilst on the other hand the venous plexus of this tissue is partially imbedded in the muscularis. The venous plexuses of the submucous tissue, like the plexus vaginalis, are to be enumerated amongst the cavernous tissues.

In Mammals, the vagina, like that of Man, is destitute of glands.

The clitoris of many Mammals, like the penis, contains cartilaginous or osseous plates, and presents the corpuscles of Pacini.

In Fishes, Amphibia, and Reptiles, no external female organs of generation are known to exist.

The mucous membrane of the cloaca is lined with ciliated epithelium in the Triton, as well as in some Batrachian Larvæ (Salamandra maculata, rana) (Leydig).

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CHAPTER XXX.

THE SPINAL CORD.

By J. GERLACH,

OF ERLANGEN.

THAT portion of the central nervous system which occupies the greater part of the vertebral canal,—the spinal cord,—forms a cylindrical column, chiefly composed of nervous tissue, and terminates in the adult with a conical extremity at the level of the first lumbar vertebra. This column presents swellings of considerable size at the points corresponding to the origin of the nerves both of the upper and lower extremities, and consists of two substances, of which the peripheric is white, whilst the central is of a grey colour.

The outer white substance has long been held to be divisible into three pairs of columns, separated from one another by the anterior longitudinal fissure, by the line of emergence of the anterior and of the posterior roots of the spinal nerves, and by the posterior longitudinal fissure. This division into anterior, lateral, and posterior columns is very distinctly marked on the surface of the spinal cord, but is gradually lost as we pass towards the central grey substance. Besides these six columns, the anterior white commissure, which is situated in front of the grey commissure (fig. 217,*f*), at the bottom of the anterior longitudinal fissure, has of late years been distinguished as a special constituent of the white substance.

The central grey substance of the spinal cord, when seen in transverse section, resembles a capital H, and is divided into a central portion, the grey commissure, with the central canal (fig. 217, *igk*); and into two lateral portions, the anterior half

of each of which is called the anterior cornu (fig. 217, *m*), whilst

Fig. 217.

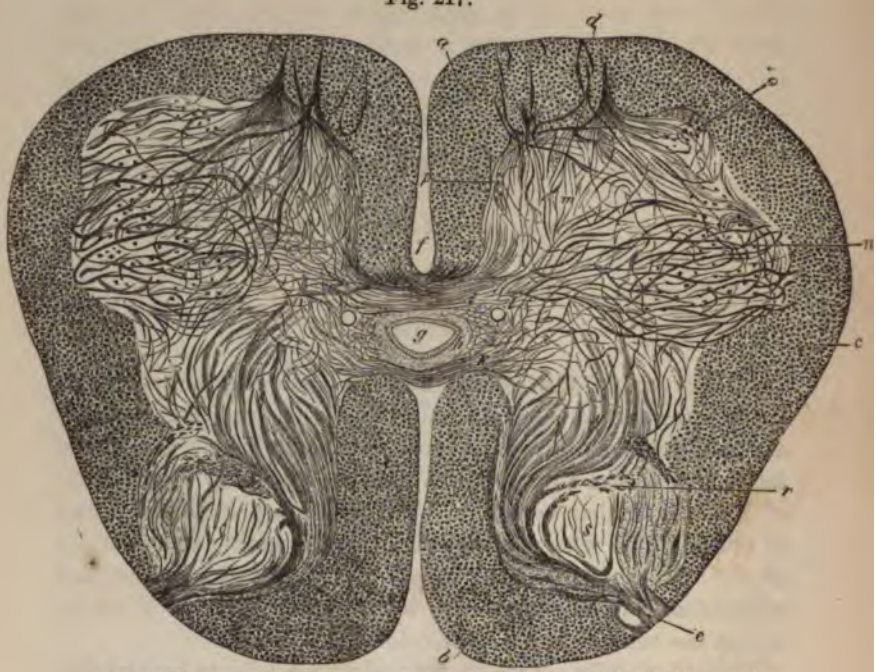

Fig. 217. Transverse section of the spinal cord of a Child six months of age, taken from the middle of the lumbar enlargement, and treated with chloride of gold and potassium, and nitrate of oxide of uranium. By means of these reagents the course of the fibres in the grey substance is rendered extraordinarily distinct. Magnified 20 diameters. *a*, Anterior column ; *b*, posterior column ; *c*, lateral column; *d*, anterior roots of a spinal nerve ; *e*, posterior root ; *f*, anterior white commissure, with fibres proceeding from the anterior white columns, and from the anterior cornua of the grey substance ; *g*, central canal, lined with epithelium ; *h*, connective tissue surrounding the central canal; *i*, transverse fibres of the grey commissure in front of the central canal ; *k*, transverse fibres of the grey commissure behind the central canal ; *l*, transverse section of the two central veins ; *m*, anterior cornu ; *n*, great lateral column of cells of the anterior cornu ; *o*, small anterior column of cells ; *p*, smallest median column of cells ; *q*, posterior cornu ; *r*, ascending column of fibres in the posterior cornu ; *s*, substantia gelatinosa.

the posterior half constitutes the posterior cornu (fig. 217, *q*).

The two lateral halves differ considerably in their configuration according to the level of the spinal cord from which they are taken; but even where these differences are most strongly expressed, as in a comparison of sections made from the

Fig. 218.

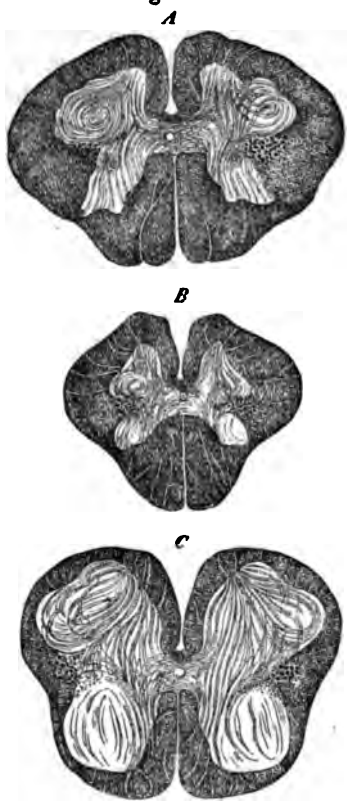

Fig. 218. Transverse section, at different heights, of the spinal cord of a Child of six months of age. Magnified 8 diameters. A, From the middle of the cervical enlargement; B, from the middle of the dorsal region; C, from the middle of the lumbar enlargement.

cervical and lumbar enlargements with other parts, they preserve the form of a large Roman H, in the dorsal region of the cord presenting narrower, and in the cervical and lumbar enlargements broader, lateral masses.

Of great importance for the understanding of the spinal cord is the proportion in point of bulk of the white to the grey substance. This is by no means identical in different parts of the organ. From a comparative examination of transverse sections made at different heights it may be clearly seen that the enlargements presented by the cord in the cervical and lumbar regions are chiefly attributable to an increase in the quantity of the grey substance. The comparison of such sections further teaches that the quantity of white substance gradually but almost imperceptibly increases, from below upwards, as is convincingly shown by a comparison of the grey and white substances in the three adjoining photographically correct sections of the human cord in the cervical, dorsal, and lumbar regions (fig 218).

In the progressively diminishing conus medullaris the white substance steadily decreases in relation to the grey matter, until where the point of the spinal cord is continuous with the filum terminale the white substance almost entirely vanishes.

The white substance of the spinal cord is composed of nerve fibres, of large and medium size, and of connective tissue and bloodvessels, whilst the grey substance contains, in addition, a large proportion of the finest nerve fibres with which I am acquainted, and which are united in a plexiform manner with nerve cells.* Of the elements that are not of a nervous nature, besides the vessels, which are found to be much more numerous in the grey than in the white substance, the capillaries forming a much closer plexus, there are present epithelial cells lining the central canal, and connective tissue, which exists in considerable quantity both in the immediate neighbourhood of the central canal (fig. 217, *b*) and in the posterior cornua, as the substantia gelatinosa of Rolando (fig. 217, *s*).

* In the dorsal region of the human spinal cord, small isolated nerve cells occur in the connective-tissue septula of that portion of the lateral column which is in close proximity to the grey substance. Such cells are very abundant in the spinal cord of the Ox and Sheep.

The White Substance of the Spinal Cord.

The white substance of the spinal cord is invested by a layer of connective tissue belonging to the pia mater. This layer remains adherent to the cord after the removal of the pia mater, and in the newly born, and in young children, can be easily torn away in long filaments, by traction from above downwards. This is attributable partly to the circumstance that this layer is directly continuous with the connective tissue of the cord itself, and partly to the fact that the direction of the fibres of the connective tissue removable with the pia mater is principally longitudinal, whilst that which remains adherent to the cord is chiefly circular. These two layers, however, are continuous with each other, and it is upon the closeness of their connection that the greater or less facility of the removal of the pia mater from the cord is dependent.* Both layers of the pia mater penetrate to the bottom of the sulcus longitudinalis anterior, that is to say, to the anterior white commissure; whilst only the deeper layer of the pia mater, which is adherent to the cord, passes in a straight direction in the sulcus longitudinalis posterior, as far as to the posterior grey commissure. This septum posterius unites the two posterior columns so firmly together that, in the strict sense of the words, we can scarcely admit the existence of a posterior longitudinal sulcus, and the conflicting views on this point may thus be reconciled.

The septum posterius is, however, not the only process that the connective tissue surrounding the spinal cord gives off

* How easily this amorphous connective tissue can be sometimes torn through I observed in the body of a Child which was sent to me some years ago, from a neighbouring town, as presenting the extraordinary feature of possessing a spinal cord that did not give origin to any spinal nerves. The vertebral canal was still unopened, but the already removed and well-preserved spinal cord was packed up with it, from which the whole pia mater, and consequently also the nerve roots, had been detached. In this otherwise exceptional instance, the whole spinal cord had been removed from the still perfect vertebral canal by traction from above, leaving the pia mater and the other membranes of the cord, with the roots of the nerves, *in situ*.

into its interior, as transverse sections show that there are numerous septulæ traversing the white substance, and penetrating to the grey, which frequently intercommunicate with each other. The difference between these septula, which enter the cord on all sides, and the septum posterius, is that the latter runs in a straight direction to the posterior grey commissure, whilst the former, branching and anastomosing like the midrib of a leaf, follow no determinate course. The connective tissue of the white substance is consequently to be regarded as a plexus of variously sized trabeculæ, in the meshes of which the nerve fibres run for the most part in a longitudinal direction. The vessels pursue the same course as the trabeculæ of the connective tissue. The size of these trabeculæ may be easily ascertained from transverse sections. The strongest, which proceed directly from the layer of connective tissue immediately investing the spinal cord, measure from 0·015 to 0·020 of a millimeter, becoming gradually attenuated by frequent subdivision, till they do not exceed 0·008 of a millimeter. The area of the more or less rhomboidal spaces bounded by these trabeculæ amounts in transverse sections to 0·03—0·09 of a square millimeter.

The layer immediately surrounding the cord, and the trabecular plexus proceeding from it, present quite peculiar structural relations, which indeed have given occasion to the establishment of a separate tissue, the so-called nerve cement, or neuroglia. The external thicker portion of the investing layer, as well as the central part of the trabeculæ arising from it, still possesses the well-known structure of fibrillar connective tissue, consisting of slightly sinuous fasciculi of the very finest connective-tissue fibrillæ, running horizontally in relation to the vertical axis of the body. After being treated with alkalies, which cause the fibrillæ to disappear, a few fine elastic fibres come into view. In chromic-acid preparations that have been treated with solution of carmine, and especially well after the addition of very dilute acetic acid, cellular elements become visible, with deeply stained nuclei, and more or less numerous and sometimes branched processes that can be relatively easily isolated, which is probably the consequence of the prolonged action of the chromic-acid compounds.

In the immediate vicinity of the connective-tissue spaces, however, the microscopical characters of the tissue undergo alteration: the fibrillæ are no longer visible; in their stead, an extremely finely granular substance makes its appearance, which is directly continuous with the fibrillated tissue, and is prolonged into the areas of the trabecular plexus, so completely filling them that only room is left for the chiefly vertically ascending nerve fibres—a relation that is most beautifully visible in thin transverse sections. In such sections the transversely divided nerve fibres appear immediately surrounded by this finely granular substance, together with not unfrequently, in certain spots, round holes, from which the sections of the nerve fibres have fallen out (fig. 219, B *c*). This finely granular substance is traversed in all directions by extraordinarily fine fibres which unite with each other into a plexus by extremely numerous communicating branches (fig. 219, A *a*). The microscopic structure of the finely granular substance, and the plexus of extremely fine fibres contained in it, only distinctly visible in the very thinnest sections, presents the closest similarity to the matrix of certain yellow or retiform cartilages, as, for example, the arytenoid cartilage of the Ox. Opinions are divided in regard to the histological value of this plexus of extremely fine fibres. Kölliker* considers it to be a plexus of stellate cells, which however are peculiar in that their processes undergo frequent subdivision, and communicate very freely, not only with each other, but with those of other and adjoining cells. Henle and Merkel† refer indeed to the similarity of this fibrous plexus to the fibrillation of fine elastic lamellæ, but classify the fibres with those of connective tissue, both on account of their size and their refractive powers in regard to light, as well as for their chemical reactions. I am unable to adopt either of these views, but regard the fibrous plexus as belonging to elastic tissue, first on account of the remarkable resemblance it presents to certain elastic or retiform cartilages, and secondly because these fibres, like those of elastic tissue, resist for a considerable period the action of alkalies.

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* *Handbuch der Gewebelehre*, 5th edition, p. 267.

† *Zeitschrift für rationelle Medicin*, 3 R., Band xxiv., p. 56.

Besides the fibrous plexus formed of the finest elastic fibres, cellular elements are also found in the finely granular matrix. These are more or less approximated at different points, and exhibit all the transitional forms from a cell nucleus invested by an extremely thin layer of protoplasm (fig. 219, B *f*) to the fully developed connective-tissue cell with its long processes (fig. 219, B *e*). After the prolonged action of an extremely dilute solution of carmine and ammonia, the nuclei of these cells, in accordance with the laws of staining of dead tissues,

Fig. 219.

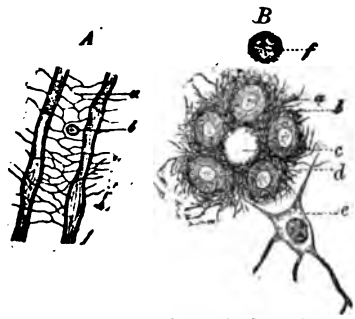

Fig. 219. A, Longitudinal section of the white substance of the spinal cord of Man; *a*, elastic fibres of the connective tissue; *b*, cellular element of the connective tissue. B, Transverse section of the white substance; *a*, axis-cylinder; *b*, medullary sheath; *c*, hole left by the falling out of a transversely divided nerve fibre; *d*, finely granular connective tissue with fine elastic fibres; *e*, a fully developed connective tissue cell, with processes; *f*, young connective tissue cell, the nucleus of which is surrounded by a very thin layer of protoplasm. Magnified 300 diameters.

become intensely coloured, the protoplasm surrounding the nucleus, and the cell processes, if present, being more faintly but still always distinctly coloured, whilst the fine fibrous plexus remains absolutely free from colour,—a fact which lends no small support to my view that this fibrous plexus belongs to the elastic tissues: for it is well known that elastic fibres remain perfectly indifferent to the methodical application of this colouring matter.

After what has been stated above, it is scarcely possible to

believe otherwise than that the tissue immediately surrounding the nerve fibres, the neuroglia, which presents the same characters also in the grey substance of the spinal cord, is a peculiarly modified form of connective tissue, the semi-solid matrix of which is finely granular instead of being fibrillated, or is even structureless, as the observations of Walther,* which were made on the frozen brains of living animals, appear to establish. If the latter be true, the finely granular character of the neuroglia must be regarded as the result of coagulation occasioned by the treatment the tissue has previously undergone with hardening agents. This finely granular or perhaps primarily structureless matrix, as is not very uncommonly the case with the ordinary fibrillated connective tissue (of serous membranes) is traversed in all directions by plexuses of fine elastic fibres, and contains cellular elements consisting of connective-tissue corpuscles in various stages of development. In regard to the occurrence of the latter, Henle and Merkel,† proceeding from the well-known observations of Cohnheim on the formation of pus, have advanced a very interesting hypothesis to the effect that they are to be regarded as escaped white corpuscles of the blood.

The nerve fibres of the white substance have as their essential constituent an axial fibre, or axis-cylinder, the diameter of which stands in tolerably constant relation to the size of the nerve fibre, amounting to about one-third or one-fourth of its breadth. In preparations that have been slightly hardened with salts of chromic acid, and subsequently treated with alkalies, the finely striated aspect of the axis-cylinder, when examined with high powers, cannot escape observation, and I entirely concur with the excellent description of the axis-fibre already given in this work (p. 154, vol. i.) by Max Schultze. A second constituent that scarcely ever fails in fully developed nerve fibres of the white substance is the nerve medulla, or medullary sheath, for the histological and micro-chemical relations of which I must likewise refer to the essay of M. Schultze. In fine sections of the spinal cord, especially after treatment with

* *Medicinische Centralblatt. Jahrg.*, 1868, p. 450.

† *Loc. cit.*, p. 79.

carmine and ammonia, the difference between the axis-cylinder and medullary sheath is most strikingly displayed. Each nerve fibre then presents the appearance of the sun as given in almanacs, the centre being an intensely red point—the axis-cylinder—which is surrounded by a broad, strongly refractile, colourless ring—the medullary sheath (fig. 219, B *a b*). Not unfrequently the medullary sheath exhibits, on transverse section, a more or less well-marked concentric striation; but I cannot determine whether this appearance is a peculiar phenomenon of coagulation, or is the result of a laminated structure in the axis-cylinder, which, as the history of its development teaches, is formed at an earlier period than the medullary sheath.

The sheath of Schwann, present in the medullated nerve fibres of the periphery, is absent in the fibres of the central organs. It is impossible to distinguish it in isolated fibres either of the grey or of the white substance, nevertheless it is within the bounds of possibility that it is not entirely deficient, but is only not brought into view in teazed-out preparations, on account of its being intimately fused with the neuroglia. In favour of this view is the circumstance that in sections of the white substance the boundary between the medullary sheath and neuroglia is indicated by a sharply defined line, which may be regarded as the expression of the sheath of Schwann, An additional argument is derived from the fact that the micro-chemical reactions of the sheath of Schwann are incontestably those of elastic tissue, and that the fine elastic fibres I have shown to be present in the neuroglia may be followed as far as to the boundary of the medullary sheath, where they often, as may be clearly seen in very thin slightly compressed longitudinal sections, end abruptly (fig. 219, A). Now, since it is impossible to admit the continuity of the elastic fibres with the medullary sheath, on account of the diversity of their micro-chemical reactions, it suggests itself to the mind as highly probable that the elastic fibres coalesce with the sheath of Schwann, which is likewise elastic, and which is fused with the neuroglia. If this view be well founded, the existence of a plexus of fine elastic fibres in the neuroglia possesses a physiological value that can scarcely be misunderstood, constituting, in fact, a protection for the nervous elements, and being ob-

viously here in place as a provision against the various movements and extensions to which the spinal cord, on account of the mobility of the vertebral column, is exposed.

I have not been able to determine satisfactorily the occurrence of division of the nerve fibres in the white substance, though other observers* have been more successful.

The diameter of the nerve fibres of the white substance is not constant, as may best be shown by a comparison of the diameter of the fibres in various regions of the spinal cord. The thickest nerve fibres, having a diameter of 0·012 to 0·020 of a millimeter, are found in that portion of the anterior columns which bounds the sulcus longitudinalis anterior. The difference in the diameter of the fibres of any given area is here also less marked. On the other hand, in the lateral columns nerve fibres may be found in one and the same area, of which some have a diameter of 0·014 to 0·018 of a millimeter, whilst others do not exceed 0·004, 0·006, and 0·008 of a millimeter. The thick fibres are more numerous in the peripheric portion of the columns, the finer ones in the more internal parts near the grey matter. The size of the fibres in the posterior columns have a certain definite relation to one another, becoming thicker the more anteriorly, *i.e.*, the nearer the posterior grey commissure they lie. In the latter region the fibres of the posterior columns have a diameter of 0·014 of a millimeter, whilst those situated more posteriorly, which become progressively finer, diminish to 0·005 and 0·008 of a millimeter. A fasciculus of fibres† that on section presents the appearance of a wedge, the point of which is directed forwards and inwards, and the thicker part backwards (see fig. 218, A),

* O. Deiters, *Untersuchungen über Gehirn und Ruckenmark*, herausgegeben von Max Schultze, 1868, p. 110. "Researches on the Brain and Spinal Cord," edited by Max Schultze.

† This was first described by Burdach as the slender fasciculus of the posterior column, and named subsequently by Kölliker, Goll's "fasciculus cuneatus," which appears to me to be a not very well selected name, since Burdach divided the posterior column of the cervical portion of the spinal cord into the slender fasciculus (*i.e.*, into Goll's "fasciculus cuneatus") and the fasciculus cuneatus, under which term he included the lateral portion of the posterior column of the cervical spinal cord after it had given off the median slender fasciculus.

is altogether composed of fine, unmingled with thick, fibres, and is found in the upper dorsal, and through the whole of the cervical, region, where it is separated off from the posterior columns towards the middle line by a strong septum. The differences in the diameter of the fibres in the spinal cord of

Fig. 220.

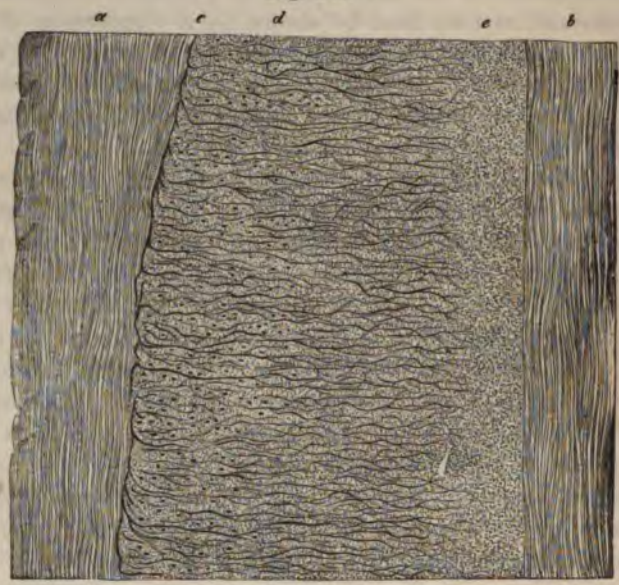

Fig. 220. Longitudinal section of one half of a spinal cord, from right to left, through the middle of the anterior cornu in the lumbar region of Man, treated with chloride of palladium and double chloride of gold and potassium, by the aid of which the fibrillation, especially of the lateral halves of the grey substance, is rendered extraordinarily distinct. Magnified 50 diameters. *a*, Lateral column; *b*, anterior column; *c*, entrance of the fibres of the anterior cornu into the lateral column, in which they ascend; *d*, lateral portion of the anterior cornu, with fibres and cells of the lateral layer; *e*, median portion of the anterior cornu.

animals is much greater than in that of Man, the greatest differences occurring in the cord of the lowest Vertebrata.

As regards the quantitative relation between the nerve fibres and the connecting neuroglia, the anterior and posterior

columns, so far as it is possible to estimate from transverse sections, contain about an equal proportion of both, except that in that part of the lateral columns which immediately surrounds

Fig. 221.

Fig. 221. Transverse section of a posterior half of the spinal cord of Man, at the level of the lumbar enlargement, treated with double chloride of gold and potassium, and exhibiting extraordinarily distinct fibrillation in the grey substance of the posterior cornu. Magnified 50 diameters. *a*, Posterior column ; *b*, lateral column ; *c*, fibrillation of the posterior cornu ; *d*, substantia gelatinosa ; *e*, roots of posterior spinal nerve, which before their entrance into the grey substance ascend, and perhaps also descend for a short distance, in the posterior column ; *g*, horizontal fibres passing from the posterior cornu into the posterior column, and from the posterior column into the posterior cornu ; *h*, fasciculi situated in front of the substantia gelatinosa, and ascending in the posterior cornu.

the grey substance the connective tissue appears to be more abundant. The posterior columns, again, are somewhat richer

in the same tissue than the anterior and lateral columns; this is especially the case with the median segment of the posterior columns of the cervical region, *i.e.*, the slender columns of Burdach and the fasciculi cuneati of Goll, which hence present a redder appearance in preparations stained with carmine than the rest of the white substance.

In regard to the direction pursued by the nerve fibres in the white substance of the cord, some are vertical, some horizontal, and others again oblique.

The vertical fibres are by far the most abundant, and constitute the chief constituent of the several columns of the cord they assume a parallel arrangement, and, united into fasciculi of various sizes, ascend to the medulla oblongata. The different fasciculi are separated from each other by connective-tissue septa, which are seen in transverse sections to proceed from the inner layer of the pia mater.

A superimposition and even an interweaving of their bands is certainly not unfrequently seen in longitudinal section; but in my opinion these appearances in the cord below the medulla oblongata are chiefly due to the extraordinary difficulty that is experienced in making a perfectly vertical longitudinal section of the cord. By far the greater number of those sections that are usually considered to be vertical are really more or less oblique, and in such it is obviously not surprising that, instead of simple apposition there should be a certain amount of super-imposition or even interweaving of the fasciculi. I have only been able to discover a true interweaving of fasciculi with certainty, and the passage of the fibres of one fasciculus into an adjoining one, in the median portion of the lateral cords.

Horizontal fibres occur in the following regions of the white substance of the cord:—

1. In the anterior white commissure, where the direction they pursue may be easily traced in transverse sections, presenting the appearance of a beautiful decussation (fig. 217, *f*, and fig. 226, *i*), though this is by no means a proof of the decussation of the anterior columns; on the contrary, according to my observations, all the horizontal fibres of the anterior white commissure that pass to the anterior column of the opposite

side, in order to ascend in them towards the cerebrum, proceed from the grey substance of the anterior cornua in such a manner that the fibres derived from the right anterior cornu ascend in the left anterior column, and those from the left anterior cornu in the right anterior column (fig. 226). In order to follow this course, the fibres must necessarily traverse the median line, and the place at which this occurs is the anterior white commissure. The fact that the white commissure is wider in those regions of the spinal cord in which the grey substance is most abundant, than in those where the grey matter is smaller, tells strongly in favour of this explanation.

2. The second place where horizontal fibres occur is in the median portions of the lateral columns close to the grey substance (fig. 220, *c*). These fibres emerge from the sides of the grey substance of the anterior cornua, and ascend in the lateral columns; at the point where they change their direction they are for a very short distance horizontal. Certain fibres of the posterior columns which are continuous with fibres of the posterior cornua lying in front of the substantia gelatinosa pursue a similar course (fig. 221, *g*). These, as sections treated with chloride of gold very distinctly show, run perfectly horizontally for considerable distances in the posterior columns. But whilst it is pretty well ascertained that the horizontal fibres of the lateral columns enter these from the grey substance, and then ascend in them, it cannot be so satisfactorily determined in the case of the horizontal fibres of the posterior columns, whether they proceed from the grey substance of the posterior cornua, and continue their course in the posterior columns, or whether they belong to that portion of the posterior roots of the spinal nerves which, before they enter the posterior cornua, ascend or descend for a certain distance in the posterior columns, and then form curves in the latter in order to penetrate into the grey substance of the posterior cornua.

3. The fibres of the posterior roots are also to be regarded as tolerably horizontal fibres of the white substance of the cord, as they run from without towards the middle line (fig. 221, *e*), and therefore appear transversely divided in sagittal longi-

tudinal sections (fig. 229, *g*). A portion of the fibres belonging to the posterior roots—namely, the lateral ones—preserve a purely horizontal course in the white substance, and run directly into the substantia gelatinosa of the posterior cornua; the middle set of the posterior root fibres, on the other hand (fig. 221, *f*), curves in that part of the posterior columns which bounds the substantia gelatinosa, and ascending in a vertical direction, and perhaps also descending for a variable distance in the posterior columns, ultimately curves again to enter the grey substance of the posterior cornua lying in front of the substantia gelatinosa (fig. 221, *g*).

The anterior roots of the nerves belong to the oblique system of fibres traversing the white substance of the spinal cord. In perfectly level transverse sections, consequently, they can only be seen in a partial and fragmentary manner (fig. 217, *d*), whilst in sagittal longitudinal sections the obliquity of their course is very apparent (fig. 229, *b*). Oblique fibres are also found in the highest part of the cervical region of the cord, and still more distinctly in the medulla oblongata. These fibres belong to the inner portion of the lateral columns, and run medially and forwards; they are, in truth, the commencement of the decussation of the pyramids, which however becomes most marked and complete in the medulla oblongata.

The Grey Substance of the Spinal Cord.

As in the white, so in the grey substance of the spinal cord, the neuroglia or tissue belonging to the class of connecting substances is abundantly present. It forms the support of the nervous elements of the grey matter, and is continuous with the similar material of the white substance. The septum posterius, however, as well as the other septula of the white columns, lose on entering the grey substance their fibrillated appearance, and assume the histological characters of that tissue which we now know to be the connecting substance occupying the interspaces of the several nerve fibres of the white substance. This tissue presents some peculiarities in the immediate neighbourhood of the central canal, and in that part also of the posterior cornua which has received the name of substantia gelatinosa, and which will be subsequently de-

scribed when the character of the several subdivisions of the grey matter are under consideration.

The nerve fibres of the grey substance are extraordinarily numerous, and form its chief constituent. Many of them possess a medullary sheath, but many must also be regarded as simply axis-cylinders, since no medullary sheath can be demonstrated around them. They differ from the fibres of the white substance by the frequent subdivision that each fibre undergoes,

Fig. 222.

Fig. 222. Partially medullated nerve fibres, with frequent division, isolated from the grey substance of the posterior cornu of a spinal cord, treated with chromate of potash. Human. Magnified 300 diameters.

and by their much smaller breadth, whilst in proportion to the number of divisions the diameter of the fibres diminishes. On this account it is not easy to furnish accurate measurements of the breadth of these fibres, since they vary from a diameter of 0·004 or 0·005 of a millimeter down to an almost immeasurable fineness, the latter being by far the most numerous. The fibres that have thus by frequent subdivision become extremely attenuated unite to form a narrow-meshed

plexus, which, together with the nerve cells, confer its peculiar characters upon the grey substance. These plexuses are not visible in the perfectly fresh spinal cord, and the application of other reagents is required to render them apparent even in spinal cords that have been treated with the salts of chromic acid. As the plexuses of these nerve fibres of the grey substance are still but little known, it will be convenient to describe shortly the mode of bringing them into view.

When it is desired to treat fine sections of the spinal cord with the double chloride of potassium and gold, some mode of hardening the tissue must be previously adopted, and for this purpose a 1 to 2 per cent. solution of double chromate of ammonia is preferable to all other preparations of chromic acid. Small portions of the perfectly fresh spinal cords of infants, macerated for fifteen or twenty days in this fluid at a low temperature, acquire a proper degree of hardness for making the section. The plexuses are shown beautifully, in proportion to the shortness of time required to harden them. For the preparation of extremely fine sections, which however do not include the whole diameter of the cord, I have employed my improved form of Welker's microtome.*

The sections should be placed in a solution containing one part of double chloride of potassium and gold in ten thousand of water that has been feebly acidified with hydrochloric acid, and in this they may be allowed to remain for ten or twelve hours, till they have slowly acquired a pale lilac colour. They should then be washed in a solution containing one part of hydrochloric acid in from 2,000 to 3,000 parts of water, and dipped for ten minutes in a mixture of 1,000 parts of a 60 per cent. solution of alcohol and one part of hydrochloric acid, then immersed for a few minutes in absolute alcohol, and finally rendered transparent in oil of cloves, and put up in Canada balsam. The plexus of nerves is even then not quite distinctly visible at first, but becomes better defined in the course of three or four hours, again blackening to so great an extent as

* J. Gerlach, *Zur Anatomie des menschlichen Rückenmarks.* "The Anatomy of the Spinal Cord of Man." *Med. Centralblatt Jahrg.*, 1867, No. 24.

to lose their sharpness of outline if the solution of gold has been too strong, or if they have lain too long in it.

The second method, which consists in a peculiar application of carmine and ammonia, has this advantage over the one above described, that the relations of the plexus of nerve fibres to the nerve cells, which are not clearly brought into view by the treatment of chloride of gold and potassium, are distinctly exhibited. For this purpose, perfectly fresh and still warm segments of the spinal cord are requisite, and may best be obtained from the Calf or Ox. Longitudinal sections, especially through the anterior nerves, and as fine as possible, are made from these with a razor;* these are immediately placed in an extremely weak solution of bichromate of ammonia (containing one part in 5,000 to 10,000 parts of water), and allowed to remain for two or three days in a cool temperature. They are then immersed in a very dilute solution of carmine and ammonia, in which they acquire, in the course of twenty-four hours, the depth of colour requisite for further preparation. And now, after being thoroughly washed with distilled water, the thinnest parts of the sections, which are at the same time the most deeply stained, are broken up with needles under a lens, when the nerve cells, which appear as darkened spots, together with the adjoining portions of the plexus of nerve fibres, may be readily isolated. The preparations may either be preserved in glycerine, or, which is still better, the water may be allowed to evaporate, and the dry object, after the addition of a small quantity of oil of cloves, may be put up in Canada balsam.

The importance of both methods for the examination of the grey substance of the spinal cord is very great, because they enable the fibres of the neuroglia, which are of equal tenuity, but are not stained either by the chloride of potassium and gold or by carmine and ammonia, to be distinguished from the true nerve fibres. Large fibres spring from the plexus of nerve fibres, that either coalesce to form still larger ones (fig. 223), and traversing the grey substance reach the white columns

* The fresher the spinal cord, the more easily are very fine sections made, as the consistence of the cord diminishes rapidly after death.

(figs. 226, 220, and 221), or attach themselves to the fasciculi of medium-sized nerve fibres contained in the posterior cornua (fig. 221, *b*).

Fig. 223.

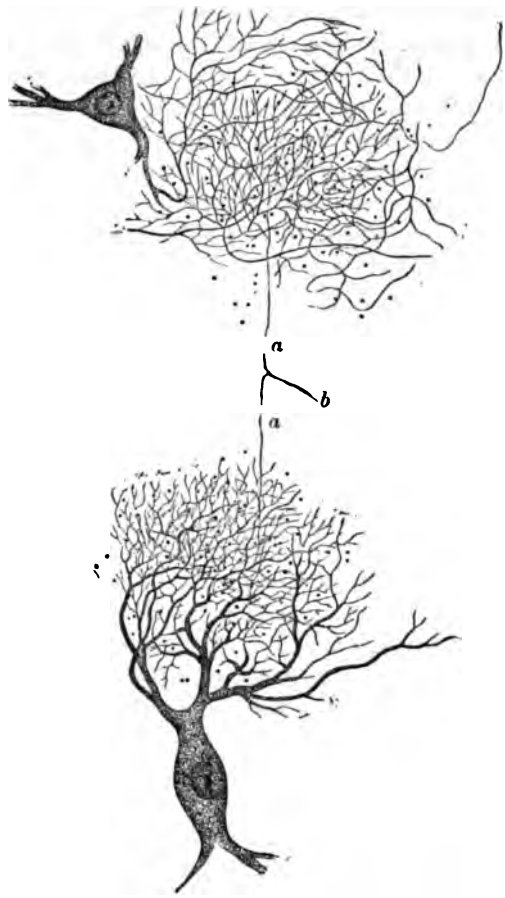

Fig. 223. A nerve fibre is here seen to divide, and the two branches to communicate with the plexus of nerve fibres that are in connection with two nerve cells. Prepared with carmine and ammonia. From the spinal cord of the Ox. Magnified 150 diameters.

The nerve cells of the spinal cord are multipolar cell bodies, destitute of any investing membrane; these contain large

homogeneous nuclei that again enclose a nucleolus with one or two vacuolæ. In many instances the cells contain pigment masses consisting of a variable number of granules, which may not unfrequently be found in the several processes. The form and size of these cells vary to an extraordinary extent, every magnitude from 0·120 of a millimeter downwards being met with. The largest cells occur in the anterior, the smallest in the posterior cornua, and those of middle size in the columns of cells which are confined to the thoracic region of the spinal cord, are situated laterally and behind the central canal, and are known under the name of Clarke's columns. Whilst we possess in the solution of carmine and ammonia, and in chloride of potassium and gold, two excellent reagents for distinguishing the delicate fibrous tissue of the neuroglia from true nerve fibres, we possess no means of establishing a sharp diagnosis between nerve cells and the cellular elements of connective tissue, since both are alike coloured by carmine and ammonia, whilst the chloride of potassium and gold exerts no action upon either. There can, indeed, be no difficulty in distinguishing between these and the larger and medium-sized nerve cells, but it is not always easy for even a practised observer to distinguish between the smallest nerve cells and certain cellular elements of connective tissue.

Two important steps have recently been made in the morphology of the nerve cells of the spinal cord. One of these is the discovery by Deiters* of the diversity in the nature of the processes of these cells, and the other is the observation made by M. Schultze† of the fibrillated character of the cell body and the cell processes. In regard to the latter point, I must refer to p. 176, *et seq.*, of the first volume of this work; the discovery of Deiters, on the other hand, demands a closer examination, since it is of the greatest importance in reference to the mode of origin of the spinal nerves.

Deiters, in the first place, observed the remarkable fact that, amongst the numerous processes given off from a nerve cell,

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* *Loc. cit.*, p. 53, *et seq.*

† *Observationes de structura cellularum fibrarumque nervearum.* Bonn, 1868.

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one always runs without division, whilst the others frequently subdivide. The unbranched process, which either springs directly from the body of the cell or from its chief and broadest process, is at its point of origin very fine, but gradually in-

Fig. 224.

Fig. 224. A nerve cell from the anterior cornu of the spinal cord of Man. *a*, Nerve process; *b*, pigment mass. Magnified 150 diameters.

creases in breadth (figs. 224 and 225); hence, in preparing isolated nerve cells, it is torn off with the greatest facility, and this is undoubtedly the reason why it so long escaped observation. In chromic-acid preparations the unbranched

process appears homogeneous, whilst the branched processes present a finely granular appearance: this difference between the two processes has however lost its significance, since it has been shown by M. Schultze that, when perfectly fresh, both the unbranched as well as the branched processes possess a finely fibrillar structure. At a variable distance from the nerve cell the undivided process becomes invested by medulla, and is thus converted into a true centric nerve fibre with medullary sheath and axis-cylinder, which last is formed by the unbranched nerve process itself. What becomes of this fibre that clearly originates from the nerve cell, whether it ascends in the white columns to the brain, or whether it constitutes a root fibre of one of the spinal nerves, has not at present been accurately determined.

Deiters took the latter view, and hence named the unbranched process the "nerve process," whilst he conferred the less happily selected name of "protoplasmic processes" to the unbranched processes, to which, however, as it has once been given, we shall adhere.

Three questions arise for the unprejudiced observer in regard to these processes: 1, What direction does the nerve process follow, and what is its ultimate destination? 2, What becomes of the protoplasmic processes? and, 3, Do all the cells of the spinal cord possess nerve processes, or are there any that give off protoplasmic processes alone?

As regards the first question, it was decidedly a happy thought of Deiters to associate the nerve process of the cells with the origin of the nerves of the spinal cord. For even if the relations between them prove to be not quite so simple as Deiters supposed, who considered that the fibres of the anterior roots originated in the cells of the anterior cornu, and those of the posterior roots from the cells of the posterior cornu, it may nevertheless be stated with an approximation to certainty that Deiters' statement is correct in regard to the origin of the anterior roots. The means of research at present at our command have not indeed permitted a nerve fibre belonging to the anterior root to be followed directly to a nerve cell; but transverse sections of the spinal cord treated with chloride of potassium and gold, and longitudinal sections

treated with carmine and ammonia, sometimes present appearances to which no other interpretation than that of Deiters can be given. In the former, the bands of fibres entering the grey substance as the anterior roots, run for the most part towards the cell layers of the anterior cornua, which they for the most part curve around. Again, fibres belonging to the anterior roots can be fairly followed into the cell layers; but it is impossible to discover their relation to the cells of which this is composed, because the chloride of gold and potassium has scarcely any action on the nerve cells, and hence in those preparations where the course of the fibres is most distinctly brought into view by the aid of this reagent scarcely any nerve cells are to be seen. On the other hand, in longitudinal sections of the spinal cord of the Calf, that have been moderately hardened in bichromate of ammonia, then well stained and carefully washed with application of gentle pressure, some of the nerve processes given off from the cells may be directly observed, and their course followed to a considerable extent. The direction pursued by these nerve processes is always horizontally forwards, whilst the frequently branched protoplasmic processes radiate outwards in every direction. In cases where I have been unsuccessful in following one of these nerve processes into the fibres of the anterior roots, its straight course towards the point of entrance of the anterior roots of the nerves, together with the fact that in the cervical and lumbar enlargements the nerve cells become more numerous coincidently with the increase in size of the root fibres, speak decisively in favour of the view that the nerve processes are to be regarded as the origins (themselves arising from the cells) of the anterior root fibres.

Far more difficult to investigate, and therefore still more obscure, is the determination of the origin of the posterior roots of the spinal nerves. The posterior cornua do not contain any more or less sharply defined cell layer, the cells being more generally distributed through a plexus of nerve fibres, and being for the most part considerably smaller than those of the anterior cornua; moreover, as has been already remarked, we have no means of distinguishing the smallest of these cells from the cellular elements of the neuroglia. Deiters has indeed demonstrated

the presence of nerve processes arising from the smaller nerve cells, which appear to belong to the region of the posterior

Fig. 225.

Fig. 225. Nerve cells from a longitudinal section of the spinal cord of a Calf, treated with carmine and ammonia. *a a*, Nerve processes running horizontally forwards. Magnified 150 diameters.

cornua, but has made no statements in regard to the direction they pursue. I have also observed these small cells, which are situated behind the cell layer of the anterior cornu, in that portion of the grey substance which can neither be held to belong to the anterior nor to the posterior cornu, to be provided with nerve processes; but have noticed in longitudinal sections, treated with carmine and ammonia, that the nerve processes of these cells also constantly run horizontally forwards; hence these smaller cells, like the larger ones of the anterior cornua, are to be regarded as points of origin of the fibres of the anterior roots. If we consider further that the number of actually visible nerve cells in the posterior cornua is smaller than in the anterior, whilst the anatomical fact has long been known that the posterior roots of the nerves are thicker than the anterior, and at the same time contain much finer fibres, and that consequently the number of fibres leaving the spinal cord by way of the posterior roots is much greater than by the anterior, it appears very improbable that the fibres of the posterior roots should have the same relations, as regards their origins, as the anterior. On the other hand, the frequent subdivision of the smaller nerve fibres, especially in those parts of the posterior cornua that lie immediately in front of the substantia gelatinosa, seems to demonstrate that the fibres of the posterior roots are not directly continuous with nerve cells, but penetrate immediately into the delicate nerve-fibre plexus of the grey substance, through the intermediation of which the relations between the fibres of the posterior roots and the nerve cells are established. If this view be correct, and many appearances obtained from preparations stained with chloride of gold are in favour of it, a fundamental morphological distinction exists between the two physiologically different species of root fibres.

In regard to the second of the above-mentioned questions, referring to the ultimate relations of the protoplasmic processes, an observation made by Deiters * may here be noticed, to the effect that the finest branches of these processes are sometimes invested by a dark-edged double contour, and

* *Loc. cit.*, p. 65.

in a few instances even undergo still further subdivision. Resting on this observation, Deiters considers these ultimate divisions of the protoplasmic processes to be indentical with the axis-cylinders of the finest nerve fibres, and to constitute a system of nerve tracts connected with the ganglion cells. Had Deiters advanced one step further, he must have discovered the fine plexus of nerve fibres of the grey substance; but as he did not apply the carminate of ammonia to his preparations, and was unacquainted with the chloride of gold method, this plexus escaped his observation. My own observations corroborate those of Deiters on this point, but I hold in addition that the finest ramifications of the protoplasmic processes ultimately participate in the formation of the fine plexus of nerve fibres which I regard as an essential constituent of the grey substance of the spinal cord. (See fig. 223.) The branches already noticed by Deiters of the finest protoplasmic processes surrounded by a double contour, are simply the commencement of this nerve-fibre plexus. The cells of the grey substance provided with nerve and protoplasmic processes are therefore *doubly* connected with the nerve-fibre elements of the spinal cord, on the one hand *by means of the nerve-process which becomes the axis-fibre of the tubules of the anterior roots, and secondly through the finest ramifications of the protoplasmic processes which constitute a part of the fine plexus of nerve-fibres of the grey substance.*

The third of the above-mentioned questions, having reference to the invariable occurrence of the nerve-process in all the ganglionic cells of the grey substance of the spinal cord, is difficult to answer, because in sections this process is only exceptionably visible; and in preparations that have been teazed out with needles the objection may always be raised that the nerve-process has been torn away at the thinner portion by which it is connected with the cell. That Deiters should extend his important discovery to all the ganglion cells of the spinal cord was natural, especially as he had demonstrated the occurrence of the nerve-process both in the larger and smaller cells. Deiters consequently did not even refer to the possibility of the occurrence of cells destitute of the nerve-process. I am of opinion, however, that a different answer may be given

to the question, as I have made a special examination of a particular group of cells of medium size situated near the centre of the medulla, and therefore about equidistant from the point of entrance of both the anterior and posterior roots into the grey substance. This group is the already-mentioned cell layer limited on each side to the cervical portion of the spinal cord, and together known as Clarke's columns. As these are not readily discoverable in the fresh spinal cord, I selected specimens that had been slightly hardened in bichromate of ammonia, but only so far as to enable transverse sections to be made. These sections were tinted with carmine and ammonia, and then placed in glycerine, in which they soon acquired a degree of hardness fitting them to be teazed out with needles. In sections of the cord thus prepared I was able with facility, under a low power, to isolate for considerable distances the nerve-process of the large cells of the anterior horns, and also of the smaller cells from the middle portion of the grey substance. In the nerve cells of Clarke's columns, on the contrary, I was unable in any one instance to discover a nerve-process. As I now possess considerable experience in this kind of investigation, and could not easily overlook the nerve-process, even if it were abruptly broken off, I believe I may say with tolerable confidence, that all ganglion cells do not possess a nerve-process. We must therefore admit the existence in the spinal cord of two morphologically different kinds of nerve cells, of which the one is in direct connection with the fibres of the anterior roots and the nerve-fibre plexus of the grey substance, whilst the other only communicates with the latter.

The idea immediately suggests itself, that these, in an anatomical point of view, sharply differentiated cells of the spinal cord possess a different physiological significance, though I do not overlook that it is always a difficult and very dubious proceeding to draw physiological conclusions from purely morphological considerations. Moreover the researches made upon the spinal cord in regard to this point are insufficient for comparison. Jacubowitsch,* it is well known, transferred the

* *Mittheilungen über den feineren Bau von Gehirn und Mark.* "Observations on the finer Structure of the Brain and Spinal Cord." Breslau, 1857.

law of Bell, which had been applied more or less successfully to the white columns of the spinal cord, to the grey substance, and maintained that the larger cells of the anterior cornua were motor, and the smaller cells of the posterior horns the sensory elements, notwithstanding that every tyro was aware that neither the conditions requisite for voluntary movements, nor those for sensation, are present in the spinal cord separated from the medulla oblongata. Hence neither the elementary parts that give the impulse for movement, nor those in which sensory impressions are perceived, can be seated in the spinal cord. Of the various centric manifestations of activity that exist in the cerebro-spinal organ, two only are present in the spinal cord, the reflectorial and the automatic. It is therefore very tempting to consider these two different modes of central activity to be associated with the two forms of cells of the spinal cord, so that the more important reflectorial actions are attributable to the more numerous cells provided with nerve processes, and the automatic actions to those which have only protoplasmic processes. In favour of this hypothesis is the circumstance also that the former of these cells, as has been rendered more than probable, stand in direct relation, by means of the nerve-process through the anterior roots, with muscles; as well as the observation of M. Schultze, according to which the fibrils constituting both the nerve-process and the protoplasmic processes of these cells do not originate in them, but only undergo rearrangement,—a fact that at least rendered in some measure intelligible, from a morphological point of view, the hitherto completely unknown process of the transference of the condition of excitation from one nerve fibre to another.

After having now acquired some knowledge of the elementary constituents of the grey substance, it only remains to describe more minutely its several portions. The median portion of the grey substance of the spinal cord, the so-called grey commissure, is composed of several distinct histological divisions. Situated slightly in front of the exact centre is the central canal (fig. 226, *c*), lined by columnar epithelial cells (fig. 226, *d*), which rest on a membrane composed of connective tissue tolerably free from nerve fibres (fig. 226, *e*). Anteriorly to this,

and immediately behind the white commissure (fig. 226, *i*), are the anterior commissural fibres of the grey substance (fig. 226, *h*). To the right and left of, as well as behind, the central canal is the fine nerve-fibre plexus (fig. 226, *f*), behind which are the posterior commissural fibres that (fig. 226, *g*) immediately bound the sulcus longitudinalis posterior

Fig. 226.

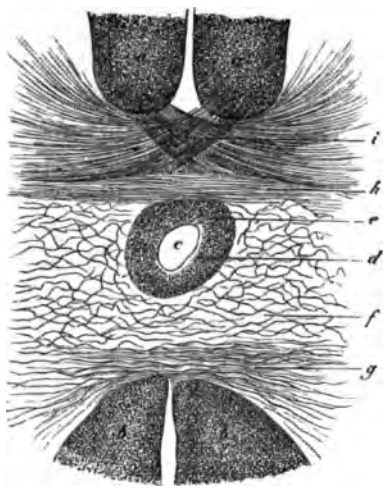


Fig. 226. Median portion of a transverse section of the spinal cord of a Child six months old, from the lower part of the cervical region, treated with double chloride of potassium and gold. Magnified 50 diameters. *a a*, Anterior columns ; *b b*, posterior columns ; *c*, central canal ; *d*, line indicating the epithelium of the central canal ; *e*, connective tissue surrounding the central canal ; *f*, nerve-fibre plexus around the central canal ; *g*, posterior transverse fibres of the grey commissure ; *h*, anterior transverse fibres of the grey commissure ; *i*, decussation of fibres in the anterior white commissure.

in the middle line, and the posterior columns laterally (fig. 226, *bb*).

The central canal is not everywhere of the same form, being somewhat oval transversely in the cervical region, whilst in the dorsal region it is more rounded, and in the lumbar region more cordiform in shape ; it commences in the floor of

the fourth ventricle, and in Man, as Stilling* has shown, extends into the conus medullaris, where it becomes progressively more posterior, ultimately terminating in the posterior longitudinal fissure. It is only completely filled with cerebro-spinal fluid in children and young people; at a later period of life it becomes contracted, and frequently, especially in the cervical region, obliterated or rather plugged up by the proliferation of epithelial cells, which begins to occur even at the age of puberty; at least, I found indications of it in the body of a man eighteen years of age. The innermost layer of tissue immediately surrounding the central canal is composed of columnar epithelial cells (fig. 227, *b*), which in children have a ciliated border,

Fig. 227.

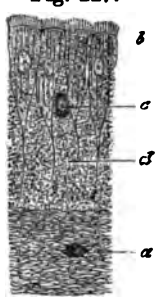


Fig. 227. Epithelium of the central canal of Man. Magnified 300 diameters. *a*, Fibrous connective tissue with a cellular element; *b*, ciliated columnar cells with fibrous appendages; *c*, ciliated cell in process of development; *d*, finely granular substance between the fibrous appendages of the ciliated cells.

though this is subsequently lost. In specimens prepared with chromic acid a thread-like process is given off from the pointed extremity of each cell, that may sometimes be traced into the fibrous connective tissue. The intervals between these appendages are occupied by a very finely granular material (fig. 227, *d*), which I consider to be a kind of connective tissue, in which there are no fine elastic-tissue plexuses. In this substance, and between the attached extremities of the columnar cells, are

* *Neue Untersuchungen über den Bau des Rückenmarks.* "Further Investigations into the Structure of the Spinal Cord." Cassel, 1857.

nuclei (fig. 227, *c*) surrounded by a thin zone of protoplasm, which become more numerous with advancing age, and can only be regarded as destined to replace the epithelial cells. Beneath the layer of finely granular substance is an extremely close plexus of fine fibres, in which also cellular elements are here and there scattered (fig. 227, *a*). I consider this tissue also to belong to the class of connective tissues, and to differ from the neuroglia elsewhere so abundant in the grey substance, only in the circumstance that the plexiform fibres already alluded to as being probably of an elastic nature (?), are present in considerable quantities. This peculiar kind of neuroglia, the so-called ependyma of the central canal, is surrounded on both sides and behind by a plexus of delicate nerve fibres, which are often brought beautifully into view in specimens prepared with chloride of gold, and amongst which small nerve cells are irregularly distributed. The meshes of this nervous plexus are here wider than in other parts of the grey substance, demonstrating the presence of a larger proportion of connective tissue in this region. Behind the plexus of nerve fibres, and immediately in front of the ependyma of the central canal, fine fasciculi of nerve fibres run horizontally across the middle line, connecting the two lateral halves of the spinal cord together, and hence named the anterior and posterior commissural fibres of the grey substance. The posterior, with the connective tissue of which the septum posterius of the pia mater is continuous, are more numerous than the anterior; both can be demonstrated with the greatest distinctness in specimens prepared with chloride of gold. The results of the experimental physiological researches of Brown-Séquard render it probable that the fine transverse fibres of the posterior grey commissure are connected with portions of the brain destined for the perception of sensory impressions, whilst the broad decussating fibres of the anterior white commissure ascend to those portions of the brain from which the impulses to voluntary movements emanate.

The two lateral portions of the grey substance of the spinal cord constitute the anterior and posterior cornua, which are not separated from one another by any sharply defined line of demarcation. The description of these parts is consequently

facilitated by admitting the existence of an intermediate portion, situated behind the anterior cornu and in front of the posterior cornu of each side. The anterior cornua are characterized by the presence of groups of large cells, of which three or more may be distinguished in the cervical and lumbar portions of the spinal cord which are more or less distinctly defined. The largest of these cell groups, which at the same time extends farthest backwards, is the lateral (fig. 217, *n*), the smallest is the median (fig. 217, *p*), whilst the third (fig. 217, *o*) is a trifle larger than this last, and is situated externally and in front of the lateral one. These groups coalesce to a greater or less extent in the anterior cornua of the thoracic region, where the number of nerve cells is considerably smaller. In the anterior cornua isolated nerve cells of variable size also occur, which do not belong to any particular cell group. These cornua are moreover traversed by broad, partly isolated, partly fasciculated nerve fibres, which, either as aiding to form the anterior roots, unite with the nerve processes of the cells, or as fibres originating in the nerve-fibre plexus, enter the anterior columns of the opposite or the lateral columns of the same half of the spinal cord. The semi-fibrous plexus is everywhere supported by connective tissue, except in the immediate vicinity of the nerve cells, which consequently, both in gold and carmine-tinted preparations that have been washed and preserved in Canada balsam, are always surrounded by a tolerably clear area, which may fairly be ascribed to the presence of unstained and therefore transparent connective tissue.

The middle part of the two lateral halves of the spinal column only contains, in the dorsal region, isolated groups of cells. These are the columns of Lockhart Clarke, to which allusion has already so frequently been made, and which are situated laterally to, and somewhat behind, the grey commissure. These groups are most strongly developed in the middle of the dorsal portion of the cord; *i.e.*, they here contain the largest number of medium-sized nerve cells. Towards the cervical as well as the lumbar regions of the cord they progressively diminish in number, and at the commencement of the cervical and lumbar enlargements altogether disappear. In gold-tinted preparations I have discovered sharply defined fasciculi of fibres closely

connected with these cell groups. On one occasion two fasciculi were given off from their anterior border, of which one, curving round, ran backwards (fig. 228, *f*), whilst the other entered the lateral columns externally, and decussated with a third fasciculus that proceeded from the centre of Clarke's group, and also ran to the side (fig. 228, *g*). If a precisely analogous arrangement of these fasciculi does not obtain throughout the entire length of the dorsal portion of the cord, fasciculi running backwards and outwards nevertheless arise through the whole extent of this region, from the columns of Clarke, with the further relations of which I am unacquainted; perhaps these, running backwards, enter the posterior

Fig. 228.

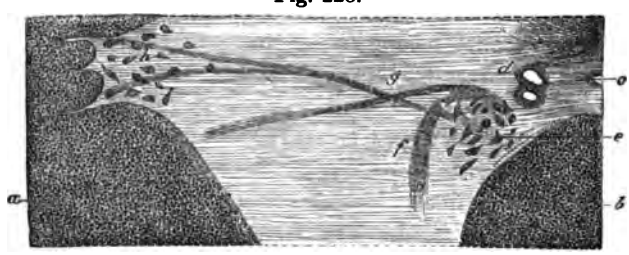


Fig. 228. Middle part of a transverse section of the spinal cord of a Child. Gold-tinted preparation. Magnified 50 diameters. *a*, Lateral column; *b*, posterior column; *c*, one half of the central canal; *d*, sections of vessels; *e*, Clarke's column; *f*, fibres from Clarke's column, running backwards; *g*, decussation of the fasciculi passing outwards; *h*, laterally situated nerve cells of variable size.

roots of the nerves. The remainder of the central portion of the cord resembles histologically those parts of the anterior cornua that are free from cells, except that, posteriorly and internally, ascending fibres occur in the grey substance, from which small fasciculi extend into the grey commissure, where they traverse the lateral parts of the posterior transverse fibres. Externally, especially in the cervical portion of the spinal cord, the line of demarcation between the grey and white substance is less sharply drawn than elsewhere, fasciculi of the lateral columns lying more or less deeply imbedded in the grey substance, and leading to the formation of the so-called reticular structure (formatio reticularis).

The posterior cornua are divisible into two portions sharply separated from each other, an anterior (fig. 221, *c*) and a posterior, which last, owing to its peculiar translucency when examined with the naked eye, has long been known as the substantia gelatinosa of Rolando (fig. 221, *d*). This part of the grey substance is the poorest in nervous elements, and is distinguished from other parts essentially by the circumstance that it does not contain the fine nerve-fibre plexus; on the other hand, it contains a large amount of connective tissue, which, however, presents certain peculiarities; for, of the three morphological constituents of the connective tissue, the finely granular matrix, the cellular elements, and the fine fibrils that I regard as elastic, the last-mentioned is present in extraordinarily small quantity, whilst the cellular elements are very abundant in the form of nuclei surrounded with a variable quantity of protoplasm. This affords an explanation of the circumstance that, in good carmine-tinted specimens, the substantia gelatinosa, next to the epithelium of the central canal, is the most deeply stained tissue. The nervous elements of the substantia gelatinosa are limited to small horizontally running fasciculi of nerve fibres which partly proceed from the posterior roots, and in part from the posterior columns; they however only traverse the gelatinous substance, pursuing a straight course through its centre, but laterally being more or less arched, and anteriorly entering that portion of the posterior cornua which possesses a nerve-fibre plexus (fig. 221, *d*). As regards, finally, the form of the substantia gelatinosa, when seen in transverse section it is an elongated oval in the cervical and dorsal regions, whilst in the lumbar it is more circular. It adjoins the posterior columns internally and rather posteriorly, as well as the posterior roots of the nerves; externally and in part also posteriorly it is invested by a thin lamina of the grey substance of the posterior horns, that possesses a nerve-fibre plexus, in which sometimes even larger nerve cells occur, and immediately anterior to which are the vertical fasciculi of the grey substance (fig. 221, *h*, and fig. 229, *d*).

The anterior division of the posterior cornua is extraordinarily rich in fibres running partly horizontally, partly vertically; the former characterized by their repeated divi-

sions, and by being traceable tolerably far forwards, part at least extending to the level of the central canal. The vertical fibres ascend for the most part in the form of a thick fasciculus in front of the substantia gelatinosa (fig. 221, *h*). This vertical fasciculus is connected with the posterior columns, and partly also with the posterior roots of the nerves, by numerous horizontal or obliquely-backward-running fibres, the greater number of which traverse the substantia gelatinosa. Successful gold-tinted preparations exhibit also fibres situated

Fig. 229.

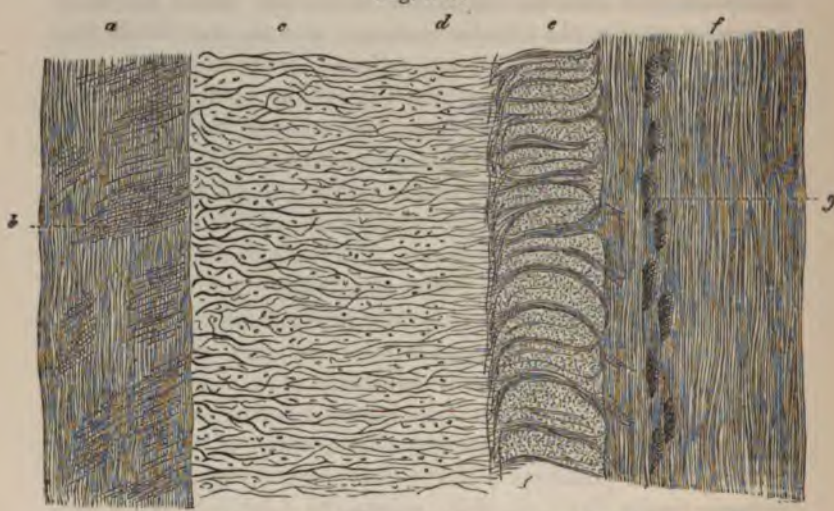


Fig. 229. Antero-posterior longitudinal section through the lumbar portion of the human spinal cord, treated with chloride of gold and potassium. Magnified 30 diameters. *a*, Anterior columns; *b*, anterior roots of the nerves traversing the anterior columns obliquely; *c*, anterior cornu; *d*, posterior cornu, with the vertical fasciculi ascending in front of the substantia gelatinosa; *e*, substantia gelatinosa, traversed by horizontal fasciculi; *f*, posterior column; *g*, posterior roots of the nerves, divided transversely in consequence of their lateral entrance.

anteriorly, which are either given off from, or unite with, this vertical fasciculus. Besides these vertical fibres, forming a single fasciculus, others pursuing a similar direction occur in the posterior cornua, which, situated more internally and fur-

ther forwards, are imbedded in the middle of the grey substance. The nerve cells of the posterior cornua are amongst the smallest, and are not, like those of the anterior cornua, collected into groups, but are distributed through that part of the posterior cornua which, like the anterior, is traversed by a fine plexus of nerve fibres.

Course of the Fibres in the Spinal Cord.

The methods of research with which we are at present acquainted are scarcely adequate to enable a precise and detailed description of the course of all the fibres in the spinal cord, which necessarily constitutes the foundation of the physiology of the organ, to be given. Nevertheless, the observations that have been already made at least permit us to draw a sketch with a tolerably firm hand of the direction pursued by the nerve fibres entering the anterior roots of the nerves, though our knowledge of the course of those forming the posterior roots is still very defective.

The fibres of the anterior roots on entering the cord traverse the white substance obliquely, without otherwise contributing to form it, and pass directly to the grey substance of the anterior cornua with the processes of the nerve cells of which they are immediately continuous; these cells are consequently to be regarded as the origins of the fibres of the anterior roots. The protoplasmic processes of these cells form parts of the fine nerve-fibre plexus of the grey substance, from which larger fibres proceed, which, running in opposite directions, leave the grey substance, and ascend to the brain in the white columns. In consequence of this constant accession of nerve fibres to the white substance, it must necessarily augment in bulk from below upwards. In regard to the course of the nerve fibres emerging from the grey substance of the anterior cornua, two sets, a median and a lateral, must be distinguished. The median enter immediately into the anterior white commissure, where they decussate with the corresponding fibres of the opposite side, and at a higher point enter the anterior column of the opposite half of the cord. The lateral fibres attach themselves to the lateral columns of their own side, in which they ascend

to the brain, previously intercrossing in the Decussatio pyramidum of the medulla oblongata.

The posterior roots of the nerves run horizontally, from without inwards, towards the middle line in the white substance of the cord, and are already here divided into two groups. The lateral and smaller one maintains its horizontal direction, and, becoming broken up into fine and still finer fasciculi, traverses the substantia gelatinosa to participate in the formation of the vertical fasciculi situated immediately on its anterior aspect, in which the fibres partly ascend and partly descend. The posterolateral root fibres, however, do not remain very long in these vertical fasciculi, but curve forwards horizontally, and thus gain that portion of the posterior cornua which possesses a fine nerve-fibre plexus.

The median and larger division of the posterior root fibres applies itself to that part of the posterior columns which bounds the substantia gelatinosa internally and posteriorly; the fibres here forming a curve, assume a vertical direction; and having reached the posterior columns, run for a considerable distance upwards, and perhaps also downwards. These median and posterior root fibres then bend once more, and again becoming horizontal, enter the grey substance of the posterior cornua, partly through the median portion of the substantia gelatinosa, and partly at its inner border. In regard to the further course of the posterior root fibres in the grey substance, no positive statements can be made, because none of the methods of research at present known enable such fibres to be distinguished from those nerve tubules that either ascend to the brain amongst the vertical fasciculi of the posterior cornua, or, passing out from the grey substance into the posterior columns, ascend to the brain. The frequent subdivision which the posterior root fibres immediately undergo on entering the posterior cornua indicates that some of them at least break up into the fine nerve-fibre plexus of the grey substance. In addition to these, however, are numerous fibres running forwards, and others passing more or less sinuously to the median line. The former may perhaps be regarded in part as posterior root fibres which subsequently and more anteriorly enter the nerve-fibre plexus; the latter, on the other hand, form commissural

fibres that traverse the middle line in the grey substance before and behind the central canal. In my opinion, these fibres entering into the posterior commissure are not to be regarded as belonging directly to the posterior roots, but as fibres passing backwards to ascend to the brain either in the vertical fasciculi of the grey substance or in the posterior columns. If this view be correct, and the analogous relations exhibited by the anterior cornua are in favour of it, the following representation or description of the course of the nerve fibres entering the grey substance through the posterior roots may be given: "A portion of the posterior root fibres break up immediately after their entrance into that part of the grey substance which possesses a nerve-fibre plexus into this plexus itself; another portion runs more forward, and as it proceeds the fibres undergo continuous subdivision and also participate in the formation of the nerve-fibre plexus. This plexus, the nodal points of which are formed by nerve cells both of large and small size, is directly continuous with the plexus of the anterior cornua. From it those nerve fibres take their origin that cross the median line in the grey commissure before and behind the central canal, then turn backwards, and ascend towards the brain, partly in the vertical fasciculi of the posterior cornua, and partly in the posterior columns, between which two last sets of fibres are manifold, but hitherto inexplicable, relations."

This description admits the complete decussation in the spinal cord of the fibres reaching it by the posterior roots: whether the decussation is really complete or only partial, a portion of the fibres originating in the nerve plexus simply running backwards towards the posterior columns, without crossing the median line, cannot be determined on purely anatomical grounds; both pathological observation, however, as well as the experimental results obtained by the most competent of all inquirers in this special research, M. Brown-Séquard, are decisively in favour of the occurrence of total decussation.

Finally, attention may here be especially called to two points.

1. The grey substance participates more freely in the con-

ductive relations of the nerve fibres entering through the posterior roots than in those that are brought to the cord through the anterior roots.

2. The morphological difference between the anterior and posterior root fibres consists in the former originating directly from the nerve cells by means of the nerve-processes, whilst the latter are only indirectly connected with the protoplasmic processes of the cells through the nerve-fibre plexus and through these processes with the cells.

CHAPTER XXXI.

THE BRAIN OF MAMMALS.

By THEODOR MEYNERT,

OF VIENNA.

General Account of the Structure of the Brain.

In the structure of the brain are united two principal features: on the one hand there is everywhere considerable uniformity in the elementary parts; on the other hand there is the utmost variety in their arrangement. It is because the significance of the elements is determined only by the particular locality in which they occur, that a purely histological description would but slightly aid the comprehension of the subject, and it is indispensable to take into account at the same time the proximate divisions of structure. Indeed, we must steadily keep in view the position of all minute details with respect to the larger masses. While we have in these considerations a justification for wandering in the following pages beyond the bounds of strictly histological fact, the compass of a manual permits in this respect of nothing more than a suggestive brevity: the more deeply inquiring student must be referred to the original sources of information. While this more discursive treatment of the morphological side allows of a more satisfactory arrangement of the subject, the reader will himself be able to aid most efficiently in making it clear, if he take with him as his guide in these difficult matters three firm and unshaken physiological principles which appear to lie at the foundation of the architecture of the brain.

1. The nerve cells possess a functional attribute; (viz., *susceptibility to impressions*). This must be regarded as a general

attribute of the centric nerve cells, it being borne in mind at the same time that it only becomes actual sensation under certain favourable circumstances.

The results of physiological inquiry do not at present justify us in confining the process of sensation to any one separate and distinct segment of the nervous system, as, for instance, to the lobes of the cerebrum. In regard to this point, the important fact must not be overlooked, that the lowest member of the vertebrate series, the Lancelet (*amphioxus*), is provided only with the central grey substance of the spinal cord. To this animal we are nevertheless not justified in denying a conscious animal existence.

On the other hand, we must not attribute the possession of any other fundamental endowment, such as, for instance, motor power, to any centric cell. The muscles alone are motor organs; and if any excitation of the nerve cell—perhaps identical with the sensory process—be able to find some paths, by traversing which it can liberate muscular energy; this arrangement will satisfactorily explain the relation of the central organ to the movements, whether such movement be immediately continuous or discontinuous, in point of time, with the excitor of sensation, and whether the conducting path simply traverses the diameter of the spinal cord, or whether it passes with an indefinite number of interruptions along the conductor-like arches of the hemispheres of the cerebrum.

2. The second postulate is *the law of Bell*, so far extended as to admit that a continuation, undisturbed by the multiplication and segmentation of the internodes, of centripetal and centrifugal conductors reaches the uppermost centres of the brain mass, or, otherwise expressed, arises from them.

3. The third postulate, lastly, is *the law of isolated conduction*, the morphological expression of which is found in the fibrillation of the white substance. And even in the grey masses, which doubtless constitute paths for transverse conduction by means of anastomoses, the law of isolated conduction holds good, though only conditionally. Here, too, it finds its morphological expression in the fact that the axes of the nerve cells appear to be elongated in the direction of the nerve fibre with which they are continuous. This fact strongly suggests

that the resistance to conduction in the direction of this axis is smaller than in the nerve-fibre plexus of the grey ganglionic mass, and that upon this depends the circumstance that the isolation of the conduction remains unimpaired.

An instructive *general survey of the leading points in the structure of the brain* may be obtained from the examination of transparent sections of the *brains of small Mammals*, which, with low powers, permit not only the relative size of the several parts, but the general arrangement of the internal structure of the organ, to be followed.

The nerve cells of the brain are collected into four principal grey masses.

1. The uppermost mass, in which originates the entire medullary portion of the brain, is the superficial grey matter of the cerebral hemispheres, or cortex of the cerebrum.

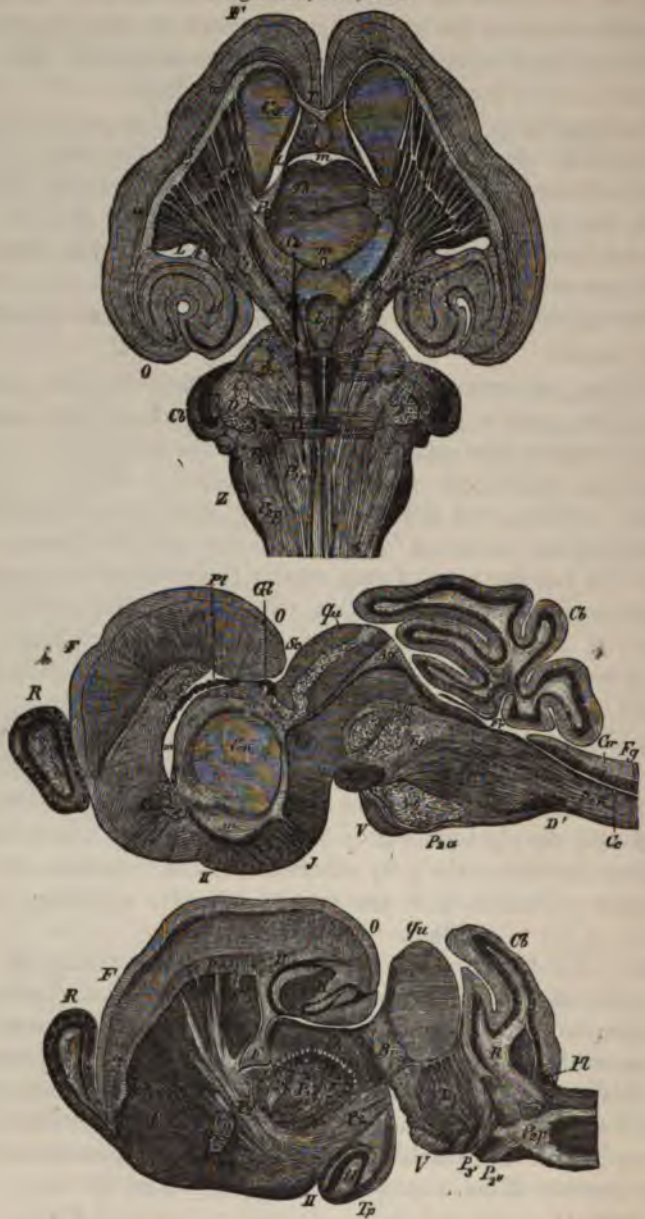
2. The second collection of grey matter is formed by the masses which, since the time of Gall, have been termed the ganglia of the cerebrum (*Corpus striatum* and *Thalamus*).

3. The tubular mass of grey matter, the persistent expression of the original form of the brain, which extends from the tuber cinereum to the conus medullaris of the spinal cord, and lines the internal surface of the central organ as the grey substance of the central cavities.

4. The grey substance of the cerebellum, which occurs partly as a superficial expansion, and partly in the form of scattered collections of cells, that on the one hand constitute the superficial and deeply seated grey masses of the cerebellum itself, and on the other the grey substance of the segments of the cerebral peduncles that are traversed by the medullary substance of the cerebellum.

In order to construct a schematic representation of the structure of the brain, the most appropriate point of departure appears to be to consider the processes of consciousness as the function of the cerebral hemispheres. Amongst other grounds for this assumption is the circumstance that the collection of all conductors in this morphological unity obviously coincides with the collection and combination of all sensory processes in the consciousness alone.

Figs. 230, 231, 232.



Figs. 230, 231, 232. *A horizontal and two antero-posterior sections of the brain of Vespertilio pipistrella, to illustrate the essential points in the structure of the brain.* General references : *F*, frontal region ; *O*, occipital region ; *Tp*, temporal region of the cerebral hemisphere, or prosencephalon (Vorderhirnes) ; *R*, olfactory lobes ; *S*, septum lucidum ; *H*, Gyrus hippocampi, with, *f*, the fornix ; *T*, the corpus callosum ; *a a*, fibræ propriæ of the cortex of the cerebrum (connecting fasciculi) ; *L*, anterior and posterior cornu of the lateral ventricle ; *Cs—Cs*, ganglionic masses of the prosencephalon (corpus striatum and lenticular nucleus, or corpus striatum internum and externum) ; *Th*, ganglionic mass of the deutencephalon (optic thalamus, Sehhügel) ; P_1, upper segment or link of the projection system for the ganglionic mass of the prosencephalon ; P_1', upper segment of the projection system for the ganglionic mass of the deutencephalon, with which also *f* (the fornix) must be included ; *Qu*, the ganglionic masses of the mesencephalon (corpora quadrigemina) ; *Br*, upper segment of the projection system of the mesencephalon (brachia of the corpora quadrigemina) ; *L p*, median portion of the floor of the mesencephalon (lamina perforata posterior) ; P_2, middle segment of the projection system, proceeding from the ganglia of the prosencephalon (crusta of the cerebral peduncle, cut off in fig. 232, on account of its inclination towards the middle line ; in fig. 231, $P_2 a$, continued through the pons) ; *Tg*, the middle segment of the projection system, proceeding from the ganglionic masses of the deutencephalon and mesencephalon (tegmentum of the crus cerebri) ; VIII, the posterior longitudinal fasciculi of the tegmentum ; *Ca*, the anterior commissure ; *Cm*, the soft commissure of the optic thalami ; *m*, the central grey substance of the cavity or ventricle of the deutencephalon (third ventricle) ; *J*, the infundibulum ; *Ag*, the grey substance of the central cavity of the mesencephalon (around the aquæductus Sylvii) ; *Gl*, pineal gland ; *Cp*, the posterior commissure ; *Sc*, the transverse fissure of the cerebrum ; *Pl*, plexus chorioideus ; *Cb*, the cerebellum ; *R*, the corpora restiformia ; *V*, the pons Varolii ; $P_2 a$, the tract of the pyramids (or continuation of the crusta of the cerebral peduncle) ; $P_2 r$, continuation of the tract of the tegmentum in the projection system of the pons and oblongata ; *Rb*, transverse section of the fasciculi of the cerebellum ; *Z*, the transverse section of the stratum zonale ; *D*, the superior olivary body ; *C*, apparent commissure of the superior olivary bodies ; *D'*, inferior olivary body ; *Fr*, the grey substance of the central cavity of the region of the opisth- and ep-encephalon forming the fourth ventricle ; *Gr*, the grey substance of the central cavity in the region of the epencephalon and spinal cord around the central canal (*Cc*) ; *Fg*, the slender fasciculus ; P_3, the inferior segment of the projection system in fig. 230, in the region of the mesencephalon, forming the nervus oculo-motorius, and in the region of the post-encephalon the nervus facialis ; in fig. 232, P_3', the fifth nerve ; P_3'', the facialis ; II, nervus opticus.

The form of the cerebral cortex, which resembles a cap covering the outer surface of the hemispheres, appears specially fitted for this comprehension of the conductive tracts (figs. 230, 231, and 232, *F, O, Tp, R, H*). This form results from the grouping of the innumerable sensory elements occupying the cortex, namely, the *nerve cells*. The sensory nerves constitute their feelers, the motor their arms. Since this convoluted mass of fibres must in great part pass through the occipital foramen in order to reach the several organs, there is a *convergence* of them from all sides, both in the peduncles of the brain and in the spinal cord, towards the grey matter of the central cavities. After however they have traversed this central grey substance, they *diverge*, as the peripheral nervous system, to all parts of the body. Since now this organization effects the contact of the sensory shell of the cortex of the cerebrum with the various forms of sensory impressions derived from the external world, the image of which is coincidently projected upon the cortex, the name of *projection system* is very appropriate to this great segment of the nervous system, and in this comparison the cortex of the cerebrum is to be regarded as the surface on which the projection is received, while the external world stands for the projected object (P_1 P_2 P_3).

As the movements of the body constitute the source of certain kinds of sensation (muscular sensations), so do they also form a part of the external world projected upon the brain. The muscular system, however, is still in another sense of the word a *projected object;* namely, through the centric and peripheric tracts of the motor nerves, along which the *cerebral cortex* reacts again upon the outer world in response to the condition of excitation induced in it by its sensory nerves.

In fig. 230, P_1 P_2 P_3 represent the successive links of the projection system, which last is interrupted several times by masses of grey matter. The first and uppermost link (P_1 P_1' and *Br*) is a medullary system springing for the most part in a radial manner from the cortex, and extending peripherically into the second principal mass of grey substance, the ganglia at the base of the hemisphere (corpus striatum and optic thalamus) (figs. 230, 231, 232, *Cs, Th, Qu*). From the interrupting network of the *ganglionic masses* springs the second

link of the projection system, the *system of the crus cerebri* (P_2), the peripheric extremity of which is found in the grey substance of the third category, *i.e.* the grey substance around the central cavities. The third link of the projection system is formed by the nerves which arise from the above-named grey substance of the central cavities, extending from the origin of the third pair of cerebral nerves in the grey matter around the aquæductus Sylvii to the nucleus of origin of the lowermost coccygeal nerves of the spinal cord. These, perhaps without exception, end peripherically in definite microscopic terminal organs that have already been described in several chapters of this work.

The region through which the *first link of the projection system* pursues its course is that formed by the cerebral hemispheres, within which it is apparently accompanied by two medullary formations, *the trabecular fibres* (*fibres of the corpus callosum*) and the *arcuate system*. While the projection system forms the medium of communication for the cells of the cortex with the outer world, the communication of the cortical cells of the cerebral hemispheres amongst themselves is accomplished in a threefold manner, so that that portion of the protoplasm of the primordial cells from which the innumerable cells of the cortex are developed, again unites to form a morphological unity; a process that can only be regarded as an instance of reunion. This view is most obviously based on the union of the transverse commissural fibres in the middle line during fœtal life, after they have perforated the median wall of the vesicles of the hemispheres. The commissural trabeculæ (callosal fibres, figs. 230 and 231, *T*) unite *the corresponding and identical regions* of the cortex of the two opposite halves of the *cerebral hemispheres*.

The different regions of the cortex of the *same* hemisphere are, on the other hand, continuously connected together by the grey fibre plexus formed by the anastomoses of the cell processes. It forms, however, the most satisfactory proof of the law of isolated conduction, which is even here in operation, that in addition the regions of the cortex are also connected together by medullated fibres (figs. 230 and 232, *aa*), the fasciculi of the fibræ propriæ, fibræ arcuatæ, which form a continuous layer, lining the inner surface of the cortex, composed of fasciculi of

variable length. As the connection of the several territories of the cortex must correspond to a functional connection of their states of excitation, through the agency of this medullary system, its fasciculi may be termed a connecting system (*Associationssytem*).

A fourth collection of medullary fasciculi belonging to the cerebral hemispheres consists of those forming a connection between the cortex of the cerebrum and the cortex of the cerebellum, which are collected in the superior peduncle of the cerebellum as a distinct band, situated superficially in the back of the pons; but from the intermediate nature of the course of these fibres between the two cortical substances, as well as from their long and close connection with the projection system of the cerebrum, it is impossible in such a general description as the present to give a clear notion of them, or to disentangle their relations.

The grey masses below the cerebral hemispheres (excluding from the second head the grey substance of the central cavities or tubular mass of grey matter) are:—

1. *Interruption masses* of the projection system, and
2. *Region of reduction* of the mass of this projection system.

Here the size of its first link, the great bulk of which (chiefly in the form of the corona radiata) enters the complex masses of the cerebral ganglia, becomes diminished to the inconsiderable dimensions of the columns of the spinal cord.

The reduction of the projection system in its course below the cerebral lobes does not affect the *total number of fibres alone*, but also *the number of the special fasciculi* that can be distinguished within its substance.

The first link of the projection system breaks up, at its point of entrance into the ganglia, into as many separate special masses as there are grey nuclei in the latter. Of such grey nuclei there are exhibited in figs. 230—232, the corpora striata and the lenticular nuciei (*Cs*) (corpora striata externa), with the radiated mass of fibres (P_1); the optic thalami (*Th*), and the corpora quadrigemina (*Qu*), with the radiated mass of fibres P_1 and *Br*); and the distinct fasciculus of the fornix (*f*), which is the projection fasciculus of the cortex for the anterior eminence of the optic thalami. Whilst the upper link of the

projection system displays a *multiplicity* of termini, *the second segment of the projection system*, the *crus cerebri* at its exit from the ganglionic masses already becomes reduced to the merely double tract, anterior and posterior, of the peduncle of the brain, *i.e.*, the crusta (figs. 230 and 232, P_2) and the tegmentum of the crus cerebri (figs. 230 and 232, *Tg*), which are continued into the anterior (figs. 231, P_2d) and posterior regions (figs. 230, 231, and 232, P_2r) of the pons and medulla oblongata, and ultimately unite into a morphologically single tract constituting the medullary investment of the medulla spinalis.

The segmentation of the projection system, its interruption by the grey masses, certainly does something more than effect the simple transference of the condition of excitation from one series of ganglion cells to another superjacent to it, like the handing of buckets from one person to another on a ladder. The morphological significance of the interruption consists in most cases in the circumstance that the intercalated cells, besides continuing the segmented but still direct centripetal or centrifugal path, constitute circuits to centres situated apart from the direct continuation of the projection system.

An exemplification of this is afforded by the centrifugal tract shown by innumerable anatomico-pathological observations to issue from the cortex of the cerebrum, and to reach the anterior nerve-roots of the spinal cord by passing through the corpus striatum and lenticular nucleus, the crusta of the crus cerebri, the pons and the anterior pyramids of the medulla oblongata (figs. 230 and 232, P_1, *Cs*, P_2; fig. 231, P_2d). The size of the crusta (Hirnschenkelfuss) of the crus cerebri above its entrance into the pons, is reduced to the small dimensions of its continuation in the projection system forming the pyramids, in consequence of a thick fascicular portion bending back into the cerebellum through the lateral portion of the pons, and thus quitting the tract of the projection system.

The tract of uniform size which passes from the cortex of the cerebrum into, for instance, the lenticular nucleus, passes likewise in this ganglion into cells from which, although there is at the same time a reduction of fibres, there still arise two subsequently diverging tracts, one running into the spinal cord, the other into the cerebellum.

The double nature of the tracts by which the projection system begins to be reduced in the crus cerebri, as crusta and tegmentum, indicates a natural division of their ganglia of origin into the ganglia of the *crusta* and the ganglia of the *tegmentum* of the crus cerebri. Of the former, the most important are the *caudate nucleus* (intra-ventricular corpus striatum) and the *lenticular nucleus* (extra-ventricular corpus striatum); of the latter, the *optic thalami*, the *corpora quadrigemina*, and the *corpora geniculata interna*. In point of size there is no necessary relation between the development of the tract of the crusta with its ganglia, and the development of the tract of the tegmentum with its ganglia; a fact which is very significant, and is the fundamental explanation of the variations in form of mammalian brains. The tract of the crusta only of the cerebral peduncle rises and falls with the development of the hemispheres, and hence Man, for example, possesses the largest lenticular nucleus and crusta of the crus cerebri. The tegmentum of the crus, with its ganglia, especially the corpora quadrigemina and corpora geniculata interna, on the other hand, are the more largely developed in proportion to the smallness of the cerebral lobes. Hence the defective proportion which, in the small cerebral-lobed brain of the Bat (figs. 230, 231, and 232), the peduncular tract (P_2, P_2a) bears to the tegmentum (Tg and P_2r). The important pathological fact that lesion of the ganglia of the crusta of the cerebral peduncle occasions complete hemiplegia and the equally noteworthy physiological experiment that on the application of an external stimulus all forms of movements occur in technically complete course, when only the ganglia of the tegmentum in the brain of the Mammal are left, speak strongly in favour of the view that the mass of the animal body is represented in the brain by a twofold projection, on the one hand by the crusta, and on the other through the tegmentum of the crus cerebri, but are only brought into relation through the pedal tract of the crus with the functional activity of the cerebral hemispheres.

The third principal mass of grey matter, the grey substance of the central cavities (as stated above, p. 374), so far from causing any reduction in the mass of fibres belonging

to the projection system, is, on the contrary, the centre for a vast increase of them, which in ordinary parlance is expressed by saying that the number of fibres belonging to the nerve roots springing from the spinal cord considerably exceeds the number of fibres of the columns of the spinal cord. This grey substance (fig. 231) commences in the region of the deutencephalon (Zwischenhirn, optic thalami) as an investment lining the third ventricle (*m*), which is rendered annular by the middle commissure (*Cm*), and which is continued into the infundibulum (*I*). In the region of the mesencephalon it surrounds the aqueduct of Sylvius (*Ag*), expands itself in the cavity of the fourth ventricle (*Fr*), and finally encloses the central canal (*Cc*) in the lower half of the medulla oblongata, and throughout the spinal cord (*Gr*). Just as in the spinal cord, the roots of the cranial nerves (P_3), representing in figs. 230 and 232 the third segment of the projection system, originate from the grey substance of the central cavities more numerous fibres than those which represent this segment in the crus cerebri. From the superficial impression obtained from fig. 230, the progress of the reduction of the projection system in the substance of the pons and upper half of the medulla oblongata is seen to be replaced by a variable amount of increase, since the circumference of this segment of the brain exceeds that of the crus cerebri. This increase of bulk depends in great measure on the interposition of grey matter that essentially accounts for the enlargement, whilst the portions of the cerebellar medullary substance which enter into the composition of the projection system diverge from this as it passes onwards, and, after forming an interweaving plexus with it, run to the cerebellum. Below the point where this occurs, the rapid diminution of the size of the medulla oblongata to that of the spinal cord corresponds also to the transition of the cerebral structure into the type of structure presented by that of the cord. In accordance with this general view, the description of the cerebral structure may be divided into the following natural sections: 1, *The lobes of the cerebrum;* 2, *The crusta or base of the crus cerebri, with its ganglia;* 3, *The tegmentum of the crus cerebri, with its ganglia;* 4, *The region of interlacement of the arms of the cerebellum;* 5, *The cerebellum;* 6, *The form-*

ation of the transitional region where the cerebral structure passes into that of the spinal cord.

1. The Cerebral Hemispheres.

The cerebral hemispheres weigh in Man from 1,100 to 1,400 grammes (16,984—21,616 grains). Their great preponderance in weight may be attributed to the circumstance that, constituting the essential seat of revived sensations or ideas, they embrace simultaneously a share of the conditions of excitation of the whole existence, whilst the functional activity of other parts of the brain is constituted only by momentary conditions of excitation.

The grey substance of the first category, the cortical grey matter of the cerebrum, invests the medulla of the hemispheres, and gives to them their external form. It presents variations in texture in different parts, on which account it is important to recollect their general form in order that these variations may be referred to their proper localities.

The cerebral hemispheres originate in the form of two laterally situated, lenticular, and hollow processes, which are budded off from the anterior cerebral vesicle. The entire superficies develops into cortical substance. The external surface of the lens is convex, like a shield; the internal surface, turned towards the constricted base or peduncle, is annular, and the lumen of the ring forms the aperture of communication between the first or anterior cerebral vesicle and the vesicle of the hemispheres. The perforation of the vesicles by the trabecular (callosal) fibres divides off a portion of the upper periphery of the ring of the median surface as the septum pellucidum. Besides this, the ring of the internal surface of the hemispheres is divisible into an anterior smaller and a posterior larger segment (or, as they may be termed, two semi-circles). The *posterior* semi-circle forms the *gyrus fornicatus*, which curves round the corpus callosum; the *anterior*, presenting an angle opening posteriorly, constitutes the *olfactory lobe*. The apex of the angle dilates to form the bulbus olfactorius; the internal and at the same time upper limb runs as the *internal* olfactory convolution into the frontal extremity of the gyrus

fornicatus; the external and at the same time lower limb of the angle, on the other hand, runs, as the external convolution of the olfactory lobe, into the temporal extremity of the gyrus fornicatus (the hooked convolution, gyrus uncinatus). Between the two limbs the inferior surface of the corpus striatum, invested by a thin layer of cortical substance, and known as the lamina perforata anterior, forms the area of the olfactory triangle.

Inasmuch as, after the removal of the olfactory lobe, the form of the internal surface of the hemispheres is essentially that of a semi-circle open in front, the *fundamentally arched form* of the latter becomes intelligible.

This *fundamentally arched* form results also in another mode from the external shield-like and unbroken surface of the vesicle of the hemispheres. A portion of the convex wall of the vesicle of the hemisphere coalesces with the external surface of a ganglion that projects from the stem or trunk of the brain into its cavity, the *lenticular nucleus* (corpus striatum externum, fig. 233, *L*), from which it results that the surface of this coalescence constitutes the only place at which the ganglionic masses and the vesicles of the hemispheres are in direct contact, without medullary union by means of the projection system (see figs. 243, 244, 245). At this point of coalescence the wall of the hemisphere remains at its thinnest, and being therefore below the level of the surrounding parts, sinks into the *Sylvian fissure.* The adhesion itself begins at the anterior border of the convexity of the hemispheres, close to that segment of the median ring which, forming the outer olfactory convolution, appears in Man as an intercalated stria of the olfactory triangular area; it then extends backwards and upwards somewhat beyond the half of the outer surface. This fissure of Sylvius (which, when the elevation of the lenticular nucleus is low, is a mere slit) represents the outer lumen of that *convexity of the hemisphere* open anteriorly, which (fig. 233) surrounds the point of its coalescence with the lenticular nucleus. The convexity is divided into an upper segment, the *frontal lobe* (*F*); a lower segment, the *temporal lobe* (*T*); and a *posterior* apical portion, the *occipital lobe* (*O*).

A capsule is thus formed from the convex external surface of the lens-shaped hemispherical vesicle, the lumen of which constitutes the cul de sac of the Sylvian fissure.

The outgrowth of the bottom of the Sylvian fissure, the *island of Reil*, constitutes a measure for the highest grades of development of the brain, because it is dependent upon the size of the lenticular nucleus, which stands in direct relation to the size of the hemispheres. This region of the cortex is connected to a remarkable extent, at the same time, with the power of speech.

The two to four primary convolutions of the Mammalian brain shape themselves from the fundamentally convex shape of the hemisphere by means of secondary parallel longitudinal grooves. (Leuret, Huschke.) The type of the brain in the Monkey (and in Man) exhibits three

Fig. 233.

Fig. 233. Antero-posterior section of the brain of the Cercocebus cinomolgus (slightly enlarged). *F*, The frontal extremity; *O*, occipital extremity; *T*, the temporal extremity; *R*, cortex of the cerebrum; *Op*, the cortex of the internal lamina of the parietal convolution, with the cortex of the insula bounding the superior fissure of Burdach; *H*, the cornu Ammonis; *S H*, sulcus hippocampi; *L*, the third segment of the lenticular nucleus; *Cl*, the claustrum; *A*, the nucleus of the amygdala; *Cs*, the tail of the corpus striatum; *P*, the cushion of the optic thalamus; *G*, external corpus geniculatum; *pr*, fibræ propriæ of two convolutions; *arc*, fasciculus arcuatus; *unc*, fasciculus uncinatus; *lg*, fasciculus longitudinalis inferior; *Ca*, anterior commissure; *inf*, inferior cornu of the lateral ventricle; P_1, upper link of the projection system.

such grooves, though there is a well-marked tendency of the most external one to split into two; and this type is also characterized by

the interruption of the middle arch by the two transverse central convolutions, and (2) by the coalescence of the inferior and middle arches near the vertex (Bischoff). The development of the convolutions of the convexity alone stands in relation to the size of the hemispheres and the higher indications of cerebral development. The development of the entire series of convolutions of the middle ring keeps pace with that of the olfactory lobes. Whilst in Man and Monkeys the *gyrus fornicatus*, compressed to the inner surface, is still completely invested by the external arch of the convex surface of the hemisphere, in brains of lower type it reaches the outer surface both at the temporal and the frontal extremity. It even may, in such cases form the whole frontal extremity of the cerebral lobe, pressing forward in front of a transverse groove (absent in Man) (fig. 238, *S*), which forms with the falciform fissure a *sulcus cruciatus* (Leuret) and covering the olfactory lobules; so that in Man and Monkeys different parts of the brain are situated behind the frontal bone than those which are there situated in other Mammals.

Within this external conformation of the cerebral cortex there appears to be—

1. A *common type* of textural lamination, characterizing the cortex of the vault of the hemispheres and that portion of the gyrus fornicatus which encircles the section of the corpus callosum. As special types may be enumerated in addition—

2. The type of the occipital apex.

3. The type of the Sylvian fissure.

4. The type of the cornu Ammonis.

5. The type of the bulbus olfactorius.

1. *The general or five-laminated type of the cortex of the cerebrum.* The first layer is principally composed of that equally punctated matrix which characterises all the grey substances of the cerebrum, and through which ganglionic cells are irregularly distributed. This matrix has been termed the ependyma formation by Rokitansky, neuroglia by Virchow, connective tissue by Kölliker, spongy substance by Deiters, and coalesced ganglion-cell substance by Henle and R. Wagner; as it occurs in the olfactory lobes and the cornu Ammonis, it has been termed gelatinous by Clarke, and molecular substance by Kupfer. Like Henle and Wagner, who have also called this layer the centric investing lamina, Stilling regards it, together

Fig. 234.

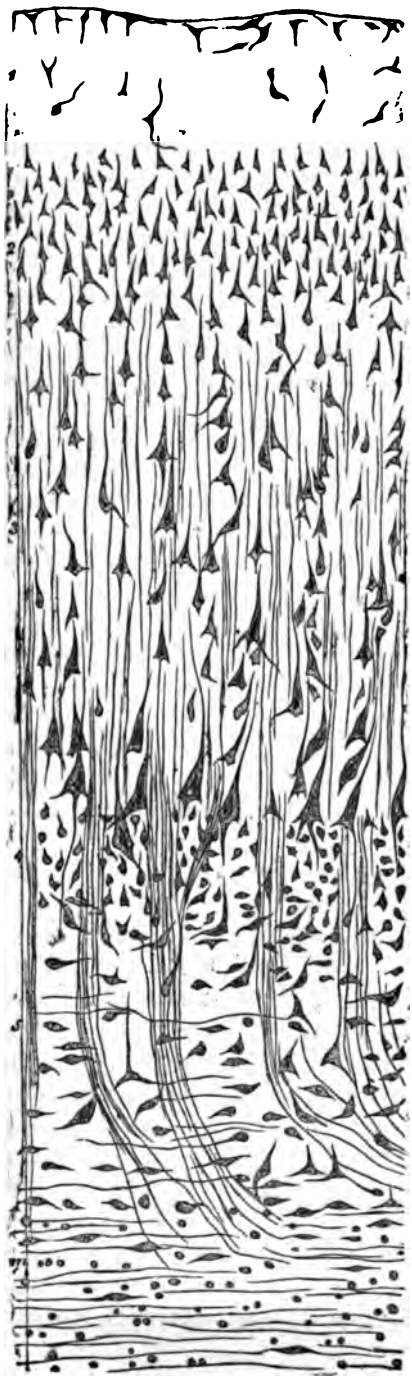


Fig. 234. Transparent section of a furrow of the third cerebral convolution of Man. Magnified 100 diameters. 1, Layer of the scattered small cortical corpuscles; 2, layer of close-set small pyramidal cortical corpuscles; 3, layer of large pyramidal cortical corpuscles (formation of the cornu Ammonis); 4, layer of small close-set irregularly shaped cortical corpuscles (granule-like formation); 5, layer of fusiform cortical corpuscles (claustral formation); *m*, the medullary lamina.

with the precisely similar layer of the cortex of the cerebellum as nervous tissue, and as being essentially a felt-like substance composed of the most indirect and finest nerve processes.

But inasmuch as we must here presuppose a certain quantitative relation between the product and the producers, *i.e.*, between the grey substance and the nerve corpuscles, which give off the processes, it would appear that this explanation is opposed by the fact, derived from comparative anatomy, that the breadth of the four internal layers of the cortex, which are rich in cells, exhibit in Mammals very variable relations to the breadth of the most external, which consists essentially of the matrix tissue (fig. 234).* Thus in Man this first layer forms only one-tenth to one-eighth; in Capuchin Monkeys, one-sixth to one-seventh; in the Dog, one-sixth; in the Cat, one-fifth; in the Bat, one-fourth; in the Calf and Roe-Deer, one-third, of the entire thickness of the cortex of the cerebrum. Moreover its absolute thickness, amounting in Man to 0·25 of a millimeter, increases in the Bat to 0·30 of a millimeter, to 0·40 of a millimeter in the Calf, and to 0·50 of a millimeter in the Roe-Deer. These facts agree much better with the view that the nerve elements of the cortex are mingled with a non-nervous matrix, the quantity of which, in the more highly organized brains, is materially reduced by the great development of the true active elements.

The nature of this matrix, which, as in the spinal cord, presents certain points of difference from the non-nervous portion of the *white* substance, determines the special characters of the grey matter. The nerve cells alone are not sufficient to give it this character; and moreover they are very numerous in some parts of the medulla (medulla of the island of Reil and of the external capsule), without indicating their presence by the greyness of the matter. The particular shade of grey in the cortex of the cerebrum, however, (putting aside the abundance

* The preparations referred to were all partially hardened in spirit, then subjected to the action of a 2 per cent. solution of bichromate of potash, then tinted with carmine, washed in alcohol, rendered transparent by means of oil of turpentine, and finally mounted in Canada balsam (Clarke's method).

of capillaries), is certainly dependent upon the accumulation of nerve corpuscles containing pigment, so that those layers through which, like the third of fig. 234, they are sparsely scattered, are recognised as more or less pale and amorphous concentric intermediate striæ.

The non-nervous grey substance consists of an amorphous and a formed portion. The diffused or amorphous material or matrix, which becomes faintly stained with carmine, exhibits a cloudiness that perhaps is only consequent upon death, and is due to the presence of dark molecules that are still seen as such with the highest powers, together with branches of the finest fibres, and are not altogether referrible to the transverse sections of those fibres. Deiters holds as an immediate consequence of the cell theory, that the matrix proceeds from a differentiation of the coalesced protoplasm of the formative cells probably occurring at the time when these have not undergone differentiation into the nervous and non-nervous tissues. He regards the free nuclei of the cerebral cortex as alone representing the formed equivalents of cells. I must, however, assert the constant presence in this organ also of cells which he admits to exist in the allied stroma of the gelatinous substance of the spinal cord and of the medulla oblongata ; viz., stellate cells, provided with a little protoplasm and a multitude of very fine branched processes. This moreover agrees with the views of Kölliker respecting the same substance. These bodies, which are in healthy states extraordinarily pellucid (and thus produce the appearance of free nuclei), assume in pathological conditions the most grotesque forms, especially in circumstances occasioning the arrest of the discharge of interstitial serum into the perivascular lymph spaces contracted in consequence of hyperæmia, but still more in degeneration of the lymphatic glands of the head and neck. Similar corpuscles form the bridge-like threads described by Roth, which, extending from the margin of the perivascular spaces, cross the lacunæ. Hence the matrix of the grey matter is traversed by a plexus of processes from non-nervous cells. The nuclei of these cells have a diameter of 9—10 μ. On the surface of the first layer of the cortex is a very delicate medullary lamina or investment of extremely fine varicose nerve fibres which decussate with one another in

all directions (Kölliker). Seen in section they do not form by themselves a definite layer; on the other hand, as Arndt has remarked, the presence of connective tissue, the fibres of which run parallel to the surface, forms a dirty opaque border only slightly stained by carmine, on the extreme margin of the cortical layer. This thin medullary lamina is developed in the gyrus uncinatus (Hakenwindung) into the far thicker stratum reticulare, and, as is clearly the case there, so probably everywhere, is composed of cell processes directed outwards. Distributed throughout the entire thickness of the outermost cortical layers are irregularly angular *nerve corpuscles* with branched processes, which are recognized as such by the well-founded criterion of Deiters, that, namely, of exhibiting at the first glance a relatively considerable proportion of protoplasm.

Bearing in mind the manifold ramification of the processes that can be exhibited by careful research, and the frequency of the anastomoses demonstrated by Arndt and Besser to occur between the processes of the cells of the cortex in certain cases, and which we may fairly conclude to be present in all, we shall be led to admit the existence of a nerve-fibre network imbedded in the grey matrix, and forming its third diffused morphological constituent. From what point of view such a general anastomotic coalescence in the territory of origin of the nerve medulla harmonizes with the phenomena of isolated conduction has been already mentioned at p. 368. In order to bring to a conclusion the preceding facts respecting the general nature of the grey cerebral substance, it may here be remarked that the nerve corpuscles are present as sharply defined elements in the grey fibre network of the cortex of the cerebrum at latest in the fifth month of embryonic development (Arndt). They are unmistakably recognized as persistent elements, by the parallelism of their axes with the radial system of fibres, which (fig. 234, 3) is so characteristic of the cortical substance.

Notwithstanding his being able to recognize the cells at so early a period, Arndt finds it possible to agree with Besser that at the time of birth the nerve corpuscles have retrograded into the transitional form of nuclei, with an ill-defined network of branches; and that the central part of this network ulti-

mately becomes converted into a secondary protoplasm. I must certainly regard this surprising statement as having been based on ambiguous specimens; for in sections of the cortex of the cerebrum of new-born children the general distribution of the most clearly defined persistent forms is readily and unmistakably exhibited.

The formation of different concentric cortical layers depends (1) upon the varying closeness of the arrangement, and (2) upon the varying forms of the nerve corpuscles. The pyramidal form (fig. 235, *a b*) of the nerve corpuscles, which is the only one admitted by some observers, as by Luys, Arndt, Stephany, is the most common in the general five-laminated type of cortical structure, and, as in fig. 234, fills the second layer, forming a

Fig. 235.

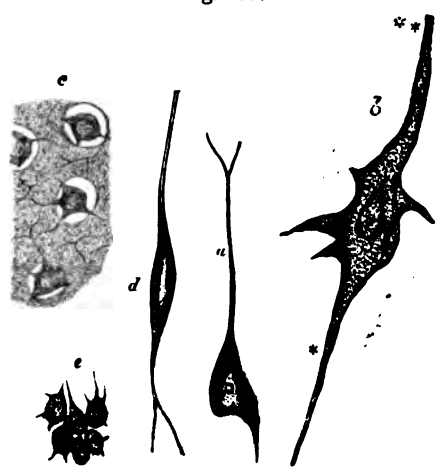


Fig. 235. *a*, Ordinary fragmentary form of the pyramidal cells, containing an angular nucleus and a branched apical process; *b*, true form of the cortical corpuscles of the second and third layers represented by a large cell of the formation of the cornu Ammonis with angular nucleus; **, truncated apical process; *, the middle basal process; *c*, the elements of the fourth cortical layer; *d*, fusiform cortical body of the fifth layer with fusiform nucleus; *e*, the elements of the so-called granule-layer of the cerebellar cortex.

closely compressed series of small elements of 10 μ in diameter; whilst in the third layer they are much more widely separated from one another, and augment progressively till they attain the

length of 40 μ. If we remember that the anterior roots of the spinal cord, at their origin in the anterior cornua, are connected with elements which, through the slenderness of their bodies, the gradual transition of these bodies into the protoplasm of the processes, and the greater number and size of the latter, are sharply differentiated from the cells in which the posterior roots originate in the interspinal ganglia, these being tumid, and provided with few and attenuated processes, an affinity in point of form is at once seen between the pyramids of the cortex and the former, which is common also to the cells of origin of all motor cerebral nerves, and permits an analogy to be drawn in regard to the significance of the pyramids of the cortex. The larger elements of the third layer deserve the special name of the *formation of the cornu Ammonis*, as they are the only morphological structures that are found in it.

The form of a simple pyramid (fig. 235, *a*) which is most frequently seen is deceptive. The true form (fig. 235, *b*) is that of a spindle, the axis of which lies in the direction of the radiating projection-fibres of the medullary portion of the convolution, and gives off an *external* strong and, according to Max Schultze (vol. i., chap. iii., p. 183), branched process (fig. 235, *a*), which runs outwards; and an *internal* more slender process directed towards the medulla of the convolution, and which, remaining, according to Koschewnikoff, undivided, forms the axis-cylinder process of Remak, M. Schultze, and Deiters. The fusiform body gives off laterally also from five to seven processes, which, like the apical process, form demonstrable anastomoses. If we make use of the term "pyramid of the cortex," then the three kinds of processes may be respectively designated (1) the process of the apex, (2) the process of the centre of the base, and (3) the process of the basal angles.

The central basal process, on account of the infrequency with which it is seen in Man, has been regarded as a monstrosity in him by Arndt, whilst he held it to be of constant occurrence in the Rat and Sheep. It is the more rarely seen because, being the process which enters the medulla, its direction is dependent on the angles formed by the fasciculi of the latter, which by no means form a straight line with the apical process of the pyramid. In sections, therefore, made parallel to the cleavage of the cortex, which is formed by the radiating lines of the apical

processes, it is so much the more frequently cut off, the greater the thickness of the whole hemisphere, and the farther the ganglionic extremity of the projection-fibre lies from the cortex. Perhaps the greater friability which characterizes the axis-cylinder processes also prevents the frequent observation of this process in preparations made by teazing out.

The nerve corpuscles of the cortex of the cerebrum are destitute of a cell wall, and Max Schultze, in chapter iii. of this work, has described their protoplasm as presenting a granular fibrous character. The younger the individual, and the more closely approximating the natural state is that in which the brain is examined, the more rarely does the protoplasm of the pyramids of the fusiform bodies to be mentioned hereafter, as well as of the irregularly shaped bodies of the first layer, contain round or oval nuclei; but, on the contrary, angular nuclei of the same shape as the protoplasm, *i.e.* of pyramidal or fusiform shape, running out into points (fig. 235, *a b d*). The angles and points of the nucleus are frequently produced into the processes of the cells, which is opposed to the view of Arndt, that these are vesicular nuclei that have been squeezed by the masses of protoplasm in accordance with their shape. If we combine the statements made by Beale, respecting the existence of a denser layer of protoplasm immediately surrounding the nucleus, with the direction of the protoplasmatic fibrillæ, described by Schultze as concentrically converging towards the processes, the idea of small similarly formed dense pyramids and spindles in the interior of a pyramidal or fusiform cell is powerfully supported. This angular included body would then be prolonged as a portion of the protoplasm into the protoplasm of the processes.

Quite independently of any interpretation of the appearances seen, I have convinced myself of the wide distribution of angular nuclei resembling the masses of protoplasm in form throughout the whole nervous centres, and Herr Ernst Fleischl has kindly furnished me with sections of the spinal cord of the Fish, containing nuclear structures similar to those I have observed in the spinal cord of Man.

The nucleoli are circular, lustrous, and in carmine prepara-

tions, as the result of a colour-contrast, are surrounded by a bluish-green halo.

Berlin has already noticed that granules and fusiform bodies occur in the cortex of the cerebrum. I have shown that these forms, intermingled with a few larger pyramidal cells, give their peculiar characters to the fourth and fifth layers of the cortex of the cerebrum. The elements of the fourth layer (fig. 235, *b*) are of irregular form, from 8 to 10 μ in diameter, rarely triangular or elongated in a direction parallel to the radial fasciculi. They are more closely arranged than in the adjoining third and fourth layers.

They remind one of the nerve corpuscles that are found in the internal granule-layer of the retina, and in the gelatinous nucleus of origin of the large root of the fifth pair of nerves.

The peculiar elements of the fifth layer, the spindle-shaped bodies 30 μ in length (fig. 235, *d*), are found least intermingled with others in the internal half of this layer, and are more scattered from this point into the medullary laminæ (*m*). At the summit of the transverse section of a convolution these fusiform bodies are vertically placed, and are parallel to the pyramids; but in the groove between two convolutions they lie horizontally (fig. 234, 5), and the pyramids stand vertically upon them. And just as the pyramids are in a line with the projection system of fasciculi, so the fusiform bodies of the fifth layer correspond in direction with the fibræ arcuatæ, which on the one hand decussate in the furrow between two convolutions with the projection fasciculi, whilst, on the other hand, in the summit of the convolution they run parallel with these fasciculi.

These fusiform cells may therefore be regarded as intercalated cells of the connecting system (Associationssystem). They may be designated the *claustral formation* (Vormauer-formation), because, as will be presently shown, the claustrum represents only a compact accumulation of cells of the innermost layer of the cortex.

They cannot however, merely on account of their fusiform shape, be considered as bipolar cells, since they also apparently

develop lateral processes, which appear to me to be in all instances directed towards the free surface of the cortex, so that there is no immediate connection of these cells with the projection system of the medulla.

The medullary portion of the convolutions becomes collected even within the cortex, beginning with the inner half of the third layer, into clearly marked radial fasciculi, which, as shown by sections, in their course through the cell masses divide them into columns. On one occasion I distinctly saw the division of a medullary fibre in the cortex, or, in other words, the formation of such a fibre from the processes of two cells. On the other hand, such a plexiform arrangement of the fibres of the medullary portion of the convolutions as has been described by Stilling in the medulla of the cerebellum certainly never occurs. Like the radial fibres, fibræ arcuatæ are also, though sparingly, found imbedded in the grey matter of the cortex. I have never observed such an accumulation of them as to cause them to form clear (in consequence of the absence of pigment) concentric markings visible to the naked eye, such as have been described by Kölliker. The medullary fibres of the central convolutions are fine, varying, according to Kölliker, from 2·6 to 6·7 μ in diameter. The connective tissue of the medulla consists of a reticulum of large connective-tissue corpuscles with thick processes, and which, more rarely than in the cortex, appear like free nuclei. These are elongated parallel to the medullary fasciculi. In the fully developed brain no finely granular substance appears to be present, but during the period of development it exists, and probably occasions the more grey than medullary aspect of the immature organ.

2. At the *summit of the occipital region*, and within the neighbouring sulcus of the median surface, which, under the name of sulcus hippocampi, forms a slight prominence with its convexity directed towards the internal wall of the posterior cornu, a different type of structure prevails. The pyramids are no longer so abundant, but are replaced by granule-like bodies. The former, which are of tolerably equal and moderate size, enter into the composition of one (the second) layer only, so that the characters of that which formed the fourth layer

occur here as the third layer; nevertheless this thick and important formation is subdivided, by the intercalation of two, poorly provided with corpuscles, intermediate granule layers, into a zone composed of five layers; so that the granule-like formation of the first-named type occurs three times. The fusiform corpuscles succeed to the innermost granule layer.

The cortex is here consequently divided into eight laminæ. The two intermediate granule layers, with sparsely scattered granules, here coalesce to form an incomparably sharply defined white layer, in consequence of the *invariable absence of pigment*, from which, on account of its tenuity, the middle granule layer is indistinguishable. In this thinly celled region a few pyramidal corpuscles, either isolated or more rarely accumulated into small groups, are found, of immense size, being at least twice as large as those of the cornu Ammonis formation (solitary cells). The brain of Monkeys, which is distinguished by excessive development of the occipital lobes, contains this type of tissue in much greater abundance than the human brain.

The formation presented by the summit of the occipital region has been taken by Clarke as the starting-point of his researches on the cortex of the cerebrum, and he gives an accurate description of the two thinly corpusculated layers. But since, like other authors, he has not distinguished between the granule-like and fusiform formations, as constituting separate layers, he fuses the external and internal granule formation with the adjoining pyramids and spindle-shaped bodies, and counts only six cortical layers, instead of eight.*

3. In the *type of the Sylvian fissure*, the third form of the cells of the cortex, the fusiform cells, predominate, forming the claustrum and amygdaloid nucleus. The claustrum, as a distinct lamina of the innermost cortical layer, and divided from the lenticular nucleus by the thin medullary lamina of the external capsule (figs. 233, 243—245, *Cl*), lines the convolutions of the island, following ina fan-like manner their inflections. Beyond the limits of the island it curves round into the cortical wall of the Sylvian fissure above, into the overhanging parietal (klapp-deckel), and below into the

* [This is evidently an error; Dr. Clarke was the first to describe eight layers in the cerebral convolutions. Proceed. Roy. Soc., Vol. xii., No. 57. TRANSLATOR.]

temporal convolutions. At the same time it extends (as is shown in fig. 233) like a clamp forwards in the frontal extremity and the temporal extremity of the primordial arch surrounding the Sylvian fissure.

The cul de sac of the Sylvian fissure, and the capsule-like vault enclosing it, constitute the form-determining centre of the convexity of the cerebrum, a region that is identical in all Mammalian brains, defined and connected together by the claustrum into one whole. It was therefore not only incontestably the right of Leuret, as the discoverer of the normal type of convolution, to supply a terminology, but it was also correct to make this the starting-point for the enumeration of the convolutions. The industrious Huschke followed him. His classification of the convolutions did not lead to the illogicality of the classification adopted since the time of Wagner, which breaks up the unity of the convolution defined by the claustrum into the terminological patchwork of a third frontal tract with a first temporal tract; and, on the other hand, since in the animal series the number of the frontal convolutions varies between two and four, assigns a varying number to the so clearly marked lowermost frontal tract.

The claustrum in frontal transverse sections of the brain (fig. 245, *Cl*), presents the form of an arched cone with its base below. This lower enlargement forms the most compact mass where the claustrum penetrates over the base of the insula into the temporal lobes. Here, constituting the anterior limit of the descending cornu of the lateral ventricle (fig. 233, *inf*), and formed from the elements of the claustrum, is a rounded mass, the amygdaloid nucleus (fig. 233, *A*), which by means of a series of transitional masses, that may be regarded as belonging either to it or to the claustrum, is continuous with the base of the latter. The whole *fusiform-cell formation*, which is expanded over the walls of the Sylvian fissure, and terminates below in the amygdala, *appears in the form of an unfolded fan, with its rays parallel to the island, and with (in the first primordial convolution) recurved borders, the handle or peduncle of which terminates in a spheroidal body, the amygdaloid nucleus.*

That this formation does not belong, "as the external corpus striatum" (Arnold), to the central ganglia, follows from its

connection (which will be afterwards shown in detail) with the fibræ propriæ of the hemisphere, since the latter are exclusively connected with cortical substance.

The continuity of the surface of the cerebral cortex, which uninterruptedly covers the nucleus of the amygdala, gives it the deceptive appearance of coalescing with a formation that is quite foreign to it, namely, with the cornu Ammonis, into a single mass, viz., the so-called *hook* of the gyrus fornicatus.

THE FORMATION OF THE CORNU AMMONIS.—The temporal portion of the gyrus fornicatus, the uncinate convolution or

Fig. 236.

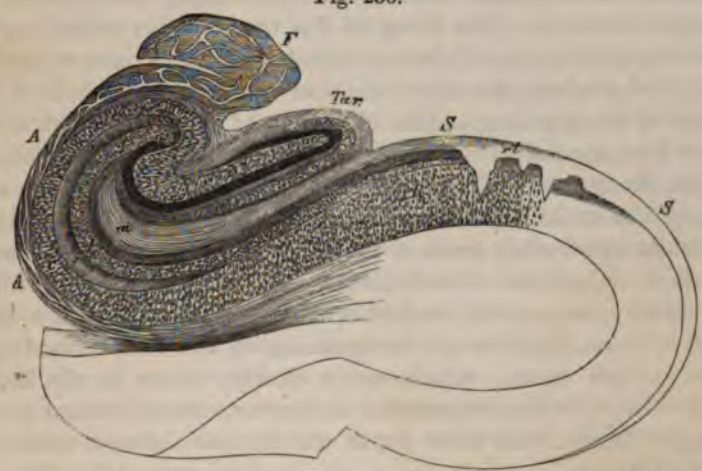


Fig. 236. Transparent transverse section from the middle of the length of the cornu Ammonis. Human. Magnified five diameters. *S*, Subiculum of the cornu Ammonis; *Tar*, fascia dentata Tarini; *F*, the fimbria; *A*, the alveus (Muldenblatt); *cc*, the stratum convolutum, with the large pyramidal bodies; *r*, the stratum radiatum; *l*, the stratum lacunosum; *m*, the nuclear lamina; *rt*, substantia reticularis; *arc*, stratum of compressed nerve corpuscles in the fascia dentata; *R*, cortex of the subiculum.

subiculum cornu Ammonis, with the cornu Ammonis, is, according to the statements made on page 378, a portion of the constricting ring of the median surface of the hemispheres, within the lumen of which the cortex terminates by a free border.

This free border is rolled inwards like the letter S throughout the greatest part of the length of the cornu Ammonis. The commencement of the inrolling is (fig. 236) the sigmoid convolution, or *subiculum cornu Ammonis*. The free margin of the median cortex, reflected back to its point of origin, is applied to it as the *fascia dentata Tarini* (*Tar*) (the rostrum of the S).

Between the subiculum (inner sharp edge of gyrus uncinatus) and the fascia dentata is the continuous grey substance of the inrolled layer (stratum convolutum, *c c*), the first fold of which (next the subiculum), covered by the medullary fibres of the trough-like lamina (alveus, Muldenblatt, *A A*), projects on the inner wall of the descending cornu, as the cornu Ammonis. The fibres of the membranous medulla of the trough-like layer (alveus) collect themselves into a band (*F*), the *fimbria*, the chief origin of the fornix. This is the third of the four longitudinal elevations of the cornu Ammonis that here appearing in section clearly develop morphologically from the process of involution. The subiculum obtains a plexiform medullary investment, analogous to the medullary element in all other parts of the cortex, in the form of the far thicker *substantia reticularis* (Arnold) (fig. 236, *rt*). This medullary investment is developed also upon the region of the stratum involutum, corresponding to the free surface of the central cortex, which, as is clearly shown in fig. 236, coincides with the involuted fold between the subiculum and fascia dentata, and there forms the *nuclear lamina medullaris* (*m*).

This involution of the cortex in a *transverse* plane, forming the cornu Ammonis, cannot, it is obvious, correspond to a *longitudinal* fold, the so-called *hook* (see p. 392). This illusory form arises from the circumstance that at the most anterior extremity of the cornu Ammonis the sigmoid-formed layer seen in fig. 236 spreads out, and only preserves a slight undulation, the summits of the waves of which project as the so-called claws (digitationes). Thus expanded, the free border of the involuted layer (seen from within) projects beyond the subiculum as the point of the hook, whilst the compressed amygdaloid nucleus in front of the cornu Ammonis (fig. 233, *H A*), rounds off the contour to the apparently recurved structure of the hook convolution.

It is only in regard to its coarser features that the cornu Ammonis presents a more complicated structure than other convolutions; but in regard to its textural lamination and the types of its cells, it is the simplest of the cerebral convolutions: in fact, a defective structure, including the pyramidal cell-forms alone of all those that are found in other parts of the cortex.

The cortex in the subiculum is composed exclusively of small and large pyramidal cells. And whilst here, on account of the absence of the fusiform cells, one form of central connection of the association systems fails, yet the other form of connection that occurs between the cortical regions, formed by the white substance of the membrana alba involvens, elsewhere scantily developed, is, by way of compensation strongly developed in the substantia reticularis. The external contour of the second cortical layer of the cerebrum appears, therefore, fenestrated (interrupted) (fig. 236, *S*), in consequence of the passage of fasciculi, of the apical processes (admitted even by Arndt to be branched) of the large pyramidal cells, which furnish their contingent to the formatio reticularis. The *involuted* layer (*c c c*) in the interior of the proper cornu Ammonis consists exclusively of the largest forms, and therefore of the pyramidal cells of the *inner half* of the third layer of the cortex. Lastly, in the region of the *fascia dentata* the small forms of cells recur closely compressed in a manner peculiar to this tissue (forming the stratum corporum nerveorum artorum), whilst in the other parts of the cortex they preserve a mean distance of 100 μ from one another. It is to this close arrangement that we must attribute the fact that Kupffer, Kölliker, and Deiters have overlooked the delicate and hazy-outlined protoplasm surrounding them, and have only noted the presence of vesicular nuclei. Hence the connective-tissue layer, *stratum granulosum*, which they admit, has no existence, and has been rightly regarded by Arndt as composed of nerve cells. Into the laminated structure of the cornu Ammonis, which is poor in nerve corpuscles, the whole thickness of the non-nervous matrix is thus introduced, producing the lamination schematically represented in fig. 237 (which should be compared with that of fig. 236). Following in the latter figure the external contour

of the cortex of the subiculum, we come to the nuclear lamina, which is thus the most external layer of cortical substance contained in the fold of involution.

1. This first cortical layer is indicated by *m*. The small scattered cells of this layer are, for the most part, recognized with difficulty, and are arranged parallel to the direction of the fibres of the nuclear lamina.

Fig. 237.

Fig. 237. Scheme of the involuted layer of the cornu Ammonis with the medulla of the alveus (Muldenblatt), and of the nuclear lamina. *m*, The nuclear lamina with very small nerve corpuscles, which is equivalent to the first lamina of the five-laminated portion of the cortex; *l*, territory of the stratum lacunosum, with a plexus formed by the apical processes of the pyramids, equivalent to the second layer; *r*, the stratum radiatum, corresponding to the outer half of the third layer; *C*, the pyramids of the involuted lamina, equivalent to the inner half of the third layer of the five-laminated cortex; *A*, lamina of the alveus, equivalent to the projection system of the medulla of the convolutions that here, on account of the absence of the granule and fusiform layer, attaches itself immediately to *C*.

2. The second layer, which contains none of the small pyramids, forms a stratum lacunosum (*l*) (stratum reticulare of Kupffer). The lacunæ marked in fig. 236, *l*, are formed by a close plexus of perivascular spaces around a series of anastomosing capillaries, by means of which the vessels of the nuclear lamina supplied from the pia mater communicate with those of the surface of the ventricle, which, proceeding from the ependyma,

form the vessels of the white substance of the trough-like layer (alveus, Muldenblatt, *A A*). In this layer the apical processes of the pyramids unite to form a nervous plexus.

3. The external half of the third layer of the cortex, the medium-sized pyramids of which are not here present, is represented, as Kupffer has remarked, by a region marked with parallel striæ, by the long apical processes of the pyramids (stratum radiatum).

Succeeding to this, the pyramids of the inner half of the third layer, arranged in numerous tiers, form the proper cornu Ammonis formation (*c*). The lacunar spaces occurring around the nerve corpuscles, which have been attributed to the retraction of the connective tissue consequent on the hardening of the preparation, are particularly visible in these large types of cells, and have been regarded by Obersteiner as *pericellular lymph passages*. He injected them, and, on making sections, found them to communicate with perivascular spaces, and to include corpuscles that he believed to correspond with undeveloped forms of lymphoid elements.

The fourth and fifth layers of other parts of the cortex are not represented in the cornu Ammonis of Man by the presence of any non-nervous substance, though in animals (Cats and Rabbits) there is certainly a layer of it, constituting Kupffer's stratum moleculare. Hence it was that Kupffer failed to see the immediate connection of the alveus with the pyramids in Man, this being effected mediately, through the stratum moleculare, in other animals. The alveus (*A*) represents the medulla belonging to the cortex of the cornu Ammonis, and, like the rest of the medullary layers of the hemisphere, is invested upon its surface by the epithelium of the lateral ventricles. The epithelium of the ventricle of the olfactory lobe has been described by Clarke as of an elongated columnar form, identical with that of the central canal of the spinal cord, the cells terminating externally in fibres that communicate with granules which Stilling alone considers to be nervous. I regard this form of epithelium as common to all cerebral ependyma, and have satisfied myself on this point in regard to the surfaces of the corpora striata, optic thalami, and corpus callosum, whilst Gerlach has established its presence in the aqueduct.

In regard to the statement made by some authors, that they have found pavement epithelium in the ventricles, it may be observed (1) that no satisfactory conclusion can be drawn from

Fig. 238.

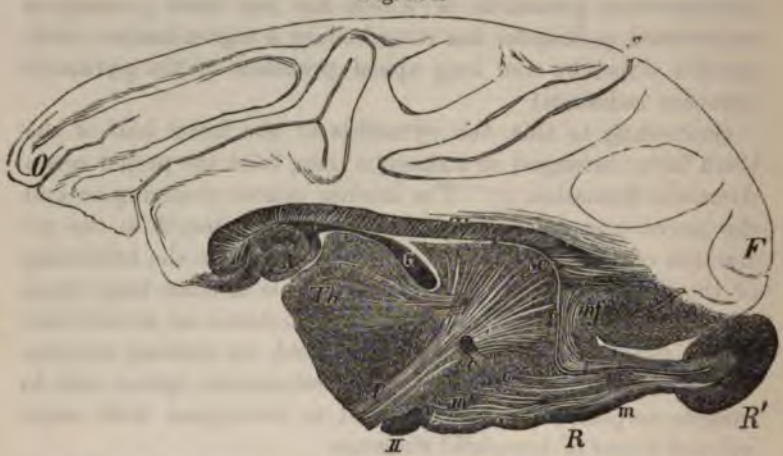


Fig. 238. Transparent sagittal section of the brain of a Dog. *FO*, The lobes of the cerebrum; *S*, the transverse limb of the sulcus cruciatus of Leuret; *F*, the frontal portion of the cerebrum, formed from the gyrus fornicatus; *R*, the olfactory lobes; *R'*, the olfactory bulb; *V V*, the cavity of the olfactory lobe in communication with the lateral ventricle; *C C*, the medullary portion of the olfactory lobe that is continuous with the anterior commissure and the transverse section of the anterior commissure which meets this medulla; the whole tract describes an arch, which for a short distance is truncated, and is directed outwards; *m*, the medulla of the bulbus olfactorius; *m'*, *m*^{1}, medulla of the olfactory lobe which enters the nucleus caudatus; *L*, basal portion of the nucleus caudatus (region of the anterior perforated plate); *N C*, head of the nucleus caudatus, continued in the form of an arch into the basal portion; *P*, pes or crusta of the crus cerebri, communicating with the caudate nucleus; *Th*, the optic thalamus, connected with fasciculi that arise from the cortex of the frontal portion of the cerebrum; *II*, optic nerve; *G*, fornix; *T*, corpus callosum; *A*, cornu Ammonis; *mf*, medulla of the olfactory lobe, running backwards into the gyrus fornicatus.

a bird's-eye view, and (2) that, in fine profile sections, the attenuated extremity of the cells, with the fibres proceeding from them, are as readily cut off as are the processes of the

nerve cells. The fifth ventricle, or camera septi pellucidi, is destitute of epithelium, like the median surface of the cerebral lobes of which it is a part.

5. THE FORMATION OF THE BULBUS OLFACTORIUS.—The anterior half-arch of the median constricting ring of the cerebrum (see p. 379) is termed the olfactory lobe, or in Man, improperly, the nervus olfactorius. It is a diverticulum of the sac of the cortex, and is hollow, like the cerebral lobes, its cavity communicating with the lateral ventricle (fig. 238, *V*). Above, its cortex is directly continuous with that of the cerebrum generally, whilst below and behind (towards the lamina perforata antica) it would immediately form a portion of the free border of the cortex, if the lamina perforata antica did not expand into an investment, to be subsequently mentioned, of cortical substance, covering the basal surface of the nucleus caudatus.

The *bulbus olfactorius* forms a cap superimposed upon this conical process of the cerebrum (fig. 238, *R'*), from the external surface of which, as is well known, are given off the nerves to the Schneiderian membrane; from its hollow internal surface proceeds a layer of medullary fibres, which invests the anterior surface of the olfactory lobe like a membrane, divides along the external and internal convolutions of the olfactory lobe, and, as seen from the basal aspect of the olfactory lobe in Man, has led to its receiving the erroneous appellation of a nerve (*m*).

The olfactory lobe divides on both sides of the anterior perforated space into an *internal* and an *external olfactory convolution*. The former is continuous with the frontal end of the gyrus fornicatus, beneath which it may be recognized for some distance as a separate longitudinal elevation (fig. 241, *Rt'*). The latter, which is the largest, coalesces with the temporal extremity of the above-described gyrus, the subiculum cornu Ammonis (fig. 242, *Ra*, *Sub*).

The bulbus olfactorius, which Luys rightly declared to be analogous to the retina, receives the brush of olfactory nerves terminating peripherically in the olfactory cells as a short projection system, just as the retina presents a still shorter projection system, to wit, the connecting fibres between the rods and cones as terminal organs, and their nervous elements

(ganglion cells of retina) as a centre. These olfactory nerves (fig. 239, *n*) extend to a *stratum glomerulosum* consisting of nodulated masses (*gl*), through the glomeruli of which some small nuclear-like cells are distributed, whilst others are scattered around them; they also contain vessels, but essentially consist of a finely granular mass resembling the matrix of the

Fig. 239.

Fig 239. Transparent section of the olfactory lobes of a Monkey. Magnified 100 diameters. *n*, The olfactory nerve layer; *gl*, the glomeruli olfactorii; *r*, the cortical substance, the ganglion cells of which are most closely aggregated internally (stratum gelatinosum; *gr*, granule layers; *m*, medullary layers.

cortex of the cerebrum. The real signification of these clumps of origin for the olfactory nerves, first observed by Leydig in the Fish, can only be estimated at their true value in Man (fig. 240), in whom the connective tissue, that in animals distends the glomerulus olfactorius to its ordinary size, is defective. Here

the entire structure appears as a knotting up of an olfactory nerve fibre, with some cells interspersed through the mass.

The peculiar reduction in the quantity of the non-nervous substance that occurs in the brain of Man, and which is here carried to the extreme, though it has already been met with in the general formation of the cortex, and in the cornu Ammonis, thus furnishes an insight into the structure of the olfactory lobes, which it would be impossible to obtain from a consideration of those of animals, in consequence of the expansion and enlargement of the curvations of the knot.

The third layer, Clarke's stratum gelatinosum (*r*), contains, in its outer zone, scattered, but in the internal zone more closely arranged, nerve cells, that are partly fusiform and partly pyramidal, and are imbedded in the matrix of the cortex. The succeeding medullary layer of the bulb exhibits a concentric alternation of pure medullary layers, with layers of small, closely arranged nerve cells, very similar to the granules of Purkinje of the cerebellum (strata granulosa et medullaria *gr*, *m*). These small irregular nerve cells perhaps differ only in point of size from the granule layers of the retina, and from the elements the fourth layer of the entire cortex of the cerebrum.

The cortex of the olfactory lobe, with the exception of the bulbus, has not as yet been examined with sufficient care to have been made the subject of a monograph. It appears to be composed of a particular form of large cells (perhaps in the manner of the cornu Ammonis).

The development of the convolution surrounding the corpus callosum, (gyrus fornicatus), which proceeds, *pari passu*, with the olfactory lobes, expresses itself by an increase of the size of the cornu Ammonis, which extends horizontally forward, lying beneath the splenium of the corpus callosum (figs. 238, 241, 242, *A* and *Ah*), and covering the optic thalamus, whilst in Man it first commences posterior to these organs. This increase causes the two cornua Ammonis to coalesce with each other in the middle line, and the same thing happens also to the fornix, throughout its whole length. Similarly, in proportion to the development of the olfactory lobes, the septa pellucida also become thickened and coalesce, with the disappearance of their so-called ventricle, by their median surfaces. The latter coalescence occurs even in the Monkeys (I do not know whether with the exception of the Pri-

mates), so that it is only in Man that the hemispheres are exclusively connected by the corpus callosum and the anterior commissure.

This cortical substance gives origin to the whole of the white substance of the cerebral hemispheres. Not even a remote approximation has yet been made to a perfect representation of this connection, in transparent sections of the brain. The absolute knowledge that we at present possess upon this point may be comprised in the following remarks :—

The medullary systems of white fibres that may in general be distinguished, have already been mentioned in the introduction

Fig. 240.

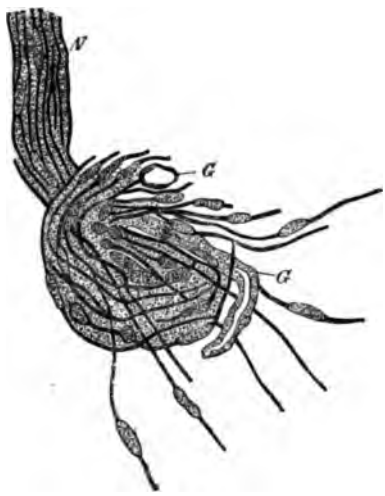


Fig. 240. A glomerulus olfactorius of Man. *N*, The entering olfactory nerve; *G*, vessels. Magnified 600 diameters.

to this chapter. They are—(1) the fibræ arcuatæ, or connecting systems; (2) the callosal system; (3) the fasciculi which pass into the medulla of the cerebellum; (4) the projection systems; and (5) the anterior commissure.

In fig. 233, the letters *pr* point to an example of the garland-like interweaving of two adjoining convolutions, by means of fibræ propriæ which surround the sulcus between them. The letters *arc* represent fasciculi that run parallel to the longitudinal axis of the hemisphere, from its occipital to its

Fig. 241.

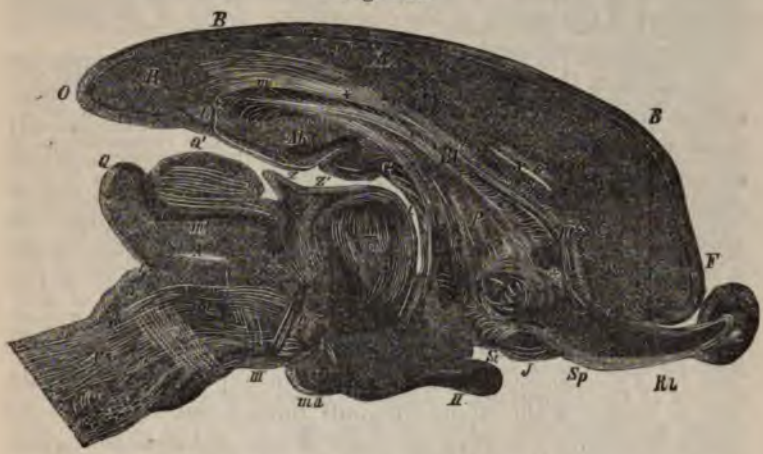


Fig. 241. Transparent sagittal section of the brain carried through the internal olfactory convolution not far from its internal surface, from the Guineapig. *F*, The frontal extremity; *O*, the occipital extremity of the cerebral lobe; *RR*, cortex; *BB*, the external layer; *S*, section of a sulcus; *Bl*, the corpus callosum; + + +, perforation of the transverse section of the callosal fasciculi by the connecting systems of the cortex of the olfactory lobe and of the gyrus fornicatus; *Sp*, superficial medullary layer of the internal olfactory convolution; *m*, fasciculi of the gyrus fornicatus; *Ah*, the cornu Ammonis; *L*, fasciculi of its formatio reticularis, which become the nerves of Lancisi; *G*, the fornix; *P*, the septum pellucidum; *St*, pedunculus septi; *J*, prolongation of the mass of the corpus striatum into the septum internal to the lamina perforata anterior; *C*, anterior commissure; *l*, cerebral ventricle; *Z*, pineal gland; *Z'*, the ganglion of the habenula; *m'*, section of the medulla of the corpora quadrigemina, which is prolonged into the posterior commissure and the pineal gland; *A*, the aqueduct; *Th*, optic thalamus; *ma*, corpus candicans (albicans); *Cx*, crus cerebri; I, the fasciculi of the tegmentum proceeding from the ganglion of the stile of the pineal gland; II, pituitary body; III, nervus oculomotorius; 8, the posterior longitudinal fasciculi; *Br*, point of decussation of the connecting arms; *Rl*, the olfactory lobe; *Rl'*, prolongation of the cortex of the internal olfactory convolution beneath the frontal extremity of the gyrus fornicatus; *QQ'*, corpora quadrigemina.

frontal extremity. They belong to the great system of the fasciculus arcuatus, which connects together the most remote provinces of the cortex of the convexity. Some of its fasciculi traverse the uppermost regions of the claustrum.

In addition the fasciculi (*unc*) of the fasciculus uncinatus are seen, which unite by the shortest path the frontal and temporal extremities of the cerebral lobes, and are concentrically surrounded by the tract of the fasciculus arcuatus, which similarly connects all the stations between the same terminal points. The fasciculus uncinatus traverses, throughout its whole extent, the mass of the claustrum and the nucleus of the amygdala. With the anterior and uncinate portion of this fasciculus are intimately united tracts of associative or connecting fasciculi in the form of flat layers, corresponding to the extent of the claustrum. They form an important part of the white matter of the island (of Reil) and the outer capsule, and there enclosing the fusiform cells of the claustral formation, unite, as do the fibræ arcuatæ, along the whole cortex with the same formation. It is only corresponding to an especially rich aggregation of the connecting systems, that there is an independent development of the innermost layer of the cortex as a special organ.

At *lg* of the same figure, fasciculi are further shown, which, constituting the *fasciculus longitudinalis inferior*, are directed from the occipital vertex towards the temporal prominence of the hemispheres. Along the median surface, as is well known, the medulla of the gyrus fornicatus encircles the corpus callosum in an arcuate manner, from the frontal to the temporal extremity of the hemispheres, and is thus for the cortex of the inner surface, analogous to the fasciculus arcuatus of the convexity. To this belongs the short medullary tract, marked *m* in fig. 241. A portion of the *medulla of the olfactory lobe* belongs also, as Gratiolet has correctly indicated, to the *fibræ arcuatæ*, since just as the cortex, both of the external and of the internal olfactory convolution, fuses with the two extremities of the gyrus fornicatus, so the medulla of the former is continuous with the medulla of the latter. These two regions of the cortex are in the first place connected by the long inferior fasciculi of the medulla of the convolution immediately covering the corpus

callosum, and known as the *nerves of Lancisi*, which are posteriorly continuous with the substantia reticularis and nuclear layer of the cornu Ammonis, and anteriorly with the grey substance of the internal olfactory convolution. Moreover the internal surface of the septum pellucidum is covered by longitudinal fasciculi which arise from the internal olfactory convolution, and emerging from it partly penetrate the genu of the corpus callosum, and partly run beneath it, traversing the body and splenium to enter every part of the course of the gyrus fornicatus. They perhaps unite with the parallel fusiform cells of the septum (fig 241, *L*, *Rf*, + + +, *m*, *Bl P*).

The superficial and the deep-seated medulla of the external olfactory convolution coalesces on the one hand with the substantia reticularis of the uncinate convolution (fig. 242, *m*, *ret*), on the other hand with the proper medullary fold of this body, which forms a moderate-sized lamina between the cortex of the hook (uncinus), and the nucleus of the amygdala (fig. 242, m^3 + *mf*). In this way *a process of the claustrum* grows into the medulla of the external olfactory convolution, through the fusiform cells of which it enters into connection with the wide-spreading connecting system of the Sylvian fissure (fig. 242, *m' Cl*).

In regard to the *system of the corpus callosum*, the microscopic investigation of transverse sections of the cerebrum of small animals, and that of the Bat in particular, which last has been carefully studied by Oellacher, demonstrates the truth of the statement made by Arnold, that the system of the corpus callosum consists exclusively of commissural fibres between corresponding and identical regions of the opposite sides of the cortex, and not, as Foville maintained, of decussating fasciculi of the projection system entering into the ganglia. It can also be shown that it does not, as Burdach believed, pass to any special convolution, but is, along with the projection system, distributed to all. Hence, as stated by Arnold and Reichert, the fasciculi of the corpus callosum and the projection fasciculi decussate in various directions. The splenium of the corpus callosum, in consequence of its inferior reflection, presents two layers (fig. 241), not a solid mass, the two laminæ of which permit the fissure of posterior and descending cornua to occur

between them, as they do not lie in contact with one another in their course towards the temporal lobes (Luys). The upper lamina of the splenium thus forms, as the tapetum, the

Fig. 242.

Fig. 242. Transparent sagittal section of the brain of the Dog through the external olfactory convolution. *F*, The frontal extremity ; *O*, the occipital extremity of the cerebral hemisphere ; *T*, transverse section of the inferior fasciculi of the body of the corpus callosum ; *Sub A*, *Sub*, occipital and temporal portions of the cornu Ammonis ; the connecting link, convex externally, between the two fragments has been cut off at the outer margin of the crus cerebri ; *Ra*, the external olfactory convolution ; *m*, the superficial medulla of the same (proceeding from the bulbus) ; *m'*, medulla of the external olfactory convolution ; *Cl*, claustrum ; L^{I}, L^{II}, L^{III}, the links of the lenticular nucleus ; *Ag*, nucleus of the amygdala ; m^{2} + *mf*, fusion of the medulla of the olfactory convolution with that of the uncinate convolution ; *Ret*, substantia reticularis fusing with the superficial medulla of the olfactory convolution ; *c*, the portion of the anterior commissure belonging to the hemisphere ; II, optic tract ; *NC*, nucleus caudatus ; *Th*, Thalamus opticus ; *P*, the foot of the crus cerebri, crusta of the peduncle.

external wall of the ventricle (Reil) (fig. 243, *T'*). The manifold and delicate interweaving of the mass of the cor-

pus callosum with foreign fasciculi may be microscopically demonstrated, and any confounding of them with connective

Fig. 243.

Fig. 243. Horizontal section of the left half of the hemisphere of Cercocebus cinomolgus. *F*, Frontal extremity; *O*, occipital extremity of the hemisphere; *FS*, entrance into the Sylvian fissure; *I*, insula; *Cl*, claustrum (vormauer); *T*, trabecula; *S*, septum; *Ca*, anterior commissure; *A*, cornu Ammonis; *V*, *Vp*, anterior and posterior cornua of the lateral venticles; *Vm*, middle ventricle; *Cm*, middle commissure; *Aq*, aquæductus Sylvii; *T'*, trabecular tapetum; *L*I, *L*II, *L*III, the segments of the lenticular nucleus; *Nc*, *Na*, head and tail of the nucleus caudatus; *Th*, mass of the optic thalamus situated in front of the corpora geniculata; *Th'*, tubercle of the optic thalamus; *Qu*,

tissue or vessels completely shut out (fig. 241). In this interlacement unmistakeably participate also, as Arnold has already remarked, fasciculi proceeding to the fornix from the posterior parts of the gyrus fornicatus, which expand over the surface of the lower half of the septum pellucidum (fig. 241, *G*).

The principal mass of the projection system, constituting the corona radiata (stab-kranz), is covered both upon its convex as well as upon its median surface by the formations of the already-named systems arising and terminating in the cortical substance. The projection system is by no means, however, composed of radiating fasciculi alone, which, like those represented in fig. 233 proceeding from the occipital apex (*P'*), penetrate directly into the ganglia, but it contains also arched portions, the most remarkable instance of which is the fornix, which represents in the optic thalamus the cortical portion of the gyrus fornicatus.

Another remarkable projection fasciculus pursuing this direction is the stria cornea, the arch formed by which connects the apex of the temporal lobe with the whole length of the internal margin of the caudate nucleus.

The number of fibres belonging to the projection system entering a ganglion from any portion of the cortex must stand in direct relation to the size of that ganglion which contains the cells in which they terminate. The large anterior cerebral ganglia of the caudate and lenticular nuclei develop by far the largest portion of their mass towards the *frontal extremity* of the hemispheres, thus constituting the *head of the corpus striatum* and the *cuneiform base of the lenticular nucleus*. Posteriorly, however, one of these ganglia runs out into an attenuated process, the other into a dentated equally thin ridge. It cannot therefore be doubted that the frontal lobes in these (which are well known to be *motor*) ganglia are represented

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corpus albicans ; *Gi*, internal corpus geniculatum ; *Ge*, external corpus geniculatum ; *m th*, fasciculi of corona radiata from the frontal lobes in the optic thalami ; *P*, crusta of the crus cerebri ; *Om*, medullary fibres proceeding from the occipital lobe to the cushion, to the arm of the superior corpora bigemina, *Bs* ; to the two corpora geniculata, the arm of the lower corpora bigemina, *Bi* ; to the crusta of the crus cerebri and to the lenticular nucleus.

by a far larger mass of the projection system than the parietal, and even yet more than the occipital and temporal lobes.

On the other hand, certain portions of the *optic thalami* and the other *centres of origin of the optic tract* are connected (and perhaps in the latter case thus only are connected) with the *occipital and temporal lobes* of the hemispheres. The latter relation may be traced in fig. 243, where the tubercle of the optic thalamus (*Th'*), the external and internal corpora geniculata (*ge* and *gi*), and the corpora quadrigemina, with their projection systems, are exposed in a horizontal section. We may here see how in the Monkey the radiating fibres proceeding from the occipital lobes converge (*Om*) in the ganglia of origin of the tractus opticus, to form a remarkably thick medullary lamina (optic radiations of Gratiolet) covered by a large number of arcuate fasciculi. This mass associates itself with the posterior and at the same time external fasciculi of the crusta of the crus cerebri. As it will be demonstrated that the *most external* fasciculus of the crusta passes through the decussation of the pyramids of the medullary oblongata into the *posterior column* of the spinal cord, it is obvious that the posterior roots of the spinal nerves are represented in the same lobes of the hemispheres as the radiations of the optic tract. Gratiolet has at the same time shown that the projection system, which according to his view proceeds from the central cortex to the optic tract, but which really penetrates its centres of origin (thalami), as well as the radiating fibres issuing from the cortex and entering the outermost fasciculus of the crusta, by no means exclusively arise from the occipital lobes, but also from the temporal lobes of the hemispheres. With these conjoined fasciculi is associated an extensive representation of still another sensory surface, namely, of the olfactory mucous membrane.

A considerable portion of the white substance of the olfactory lobe (fig. 238, m^3c) traverses the mass of the corpus striatum, and extends as far as the transverse section of the anterior commissure (*c*), which meets it in the opposite direction. This passage of the white substance of the olfactory lobe into the anterior commissure has the form of an arch convex outwards, which in the figure is for a short distance

cut off by the section. On the other hand, the fact was already known to Burdach and Gratiolet, that the fasciculi of the anterior commissure run into no part of the cortex except that of the occipital and temporal lobes. There are accordingly represented in the two last-named parts of the brain hemispheres (1) the sensory surfaces connected with the spinal cord; (2) the retina; and (3) the olfactory bulb. These lobes accord-

Fig. 244.

Fig. 244. Transparent section from the upper trunk ganglia and the insula of Man, at the height of the anterior commissure (close behind the posterior border of the orbital convolutions and the olfactory lobe). *I*, Insula; *Cl*, claustrum; *Ce*, external capsule; *L*III, third link of the lenticular nucleus; *Nc*, caput of the corpus striatum; *Nc'*, base of the head of the corpus striatum above the lamina perforata antica; *M*, medulla of the cerebral lobe (foot of the corona radiata); *Ci*, internal capsule; *Cα*, median portion of the anterior commissure; *M'*, portion of the anterior commissure belonging to the hemisphere; *R*, portion of the anterior commissure belonging to the olfactory lobe.

ingly contrast with the frontal lobe; which is chiefly connected with the motor ganglia. The foregoing statements exhaust our knowledge of the connection with the cortex of the brain of the following parts, viz., that part of the radiations of the optic tract which enters the corpora geniculata; the anterior commissure; and the above-named representation of the posterior columns in the crusta.

The mass of medullary substance proceeding from the olfactory lobes to the anterior commissure is in animals much larger than the radiations which pass into that commissure from the medulla of the hemisphere (figs. 238, *cm*²; 242, *c*). The reverse occurs in Man, in whom the anterior commissure almost entirely passes into the medulla of the hemispheres, whilst corresponding to the feeble development of the olfactory lobe is its small connection with them (fig. 241, *Ca M' R*).

Thus, besides, the decussation between the olfactory lobe of one side and the opposite hemisphere, which is effected by the cord-like convoluted course of the fasciculi (Burdach), in the anterior commissure there must necessarily also be commissural fasciculi connecting together both the two olfactory lobes and the two hemispheres.

If we include amongst these the fasciculi proceeding from the olfactory lobe to the corpus striatum of the same side (Clarke, Walter, Gratiolet), we shall have in the medulla of the olfactory lobes, which forms one body with the anterior commissure, all the variations in the course of fibres that were ascribed by Johann Müller to the chiasma nervorum opticorum. Thus the analogy between the olfactory lobes and retina is rendered still more close by the presence of an olfactory chiasma corresponding to that of the optic nerves.

The Crusta of the Cerebral Peduncle and its Ganglia.

The upper link of the projection system penetrates by its peripheric extremity into a variously formed mass of ganglia, which genetically belong (1) to the vesicles of the hemispheres, and (2) to the anterior and median cerebral vesicles. Each of these ganglia possesses two morphological poles; a central, which receives the upper link of the projection system, and a peripherical, which gives origin to the central extremities of the fasciculi of the second link of the projection system of the crus cerebri. The crus cerebri, both in its crusta (Fuss), and in the tegmentum (Haube), independently of the fasciculi of the spinal cord arising from it, contains also a considerable quantity of cerebellar fibres, which become detached from it above the spinal cord. However peculiar may be the cha-

racters presented by each of the cerebral ganglia in regard to their form and structure, those connected with the crusta and those with the tegmentum still exhibit certain features in common, and hence the natural basis of division for the ganglia rests upon the double nature of their peripheric connection. The *corpora geniculata* (Kniehöcker) alone, since they do not stand in connection with the crus cerebri, occupy an independent position as appendages of the ganglia of the tegmentum.

The ganglia of origin of the crusta of the crus cerebri are, (1) the nucleus caudatus; (2) the nucleus lenticularis; and (3) the substantia nigra of Soemmerring, between the crusta and tegmentum of the crus cerebri.

The *caudate nucleus* runs as an arch concentric to the hemispheres around a transverse axis lying in the crus, an axis which is physically embodied by the transverse wedge of the lenticular nucleus (corpus striatum externum), the base of which is turned outwards, and the point inwards. This relation between the two ganglia is displayed in fig. 243. The frontal segment of the arch of the corpus striatum, lying in front of the lenticular nucleus (*L*I, II, III) forms the large head (*Nc*), and the segment belonging to the occipital and temporal lobes, the thin tail (*Na*). The transverse and arcuate ganglia of origin of the crusta of the crus cerebri, moreover, coalesce at the frontal extremity of the arch of the corpus striatum, by the junction of the caput with the third link of the lenticular nucleus (fig. 244, *Nc' L*III), and they also coalesce at the temporal extremity of this striated arch (fig. 233, *Cs L*). In order to understand the anterior coalescence, it must be borne in mind that the arch of the caput of the corpus striatum curves over that surface of it which is apparent in the lateral ventricle, downwards and outwards to the basis of the cerebrum, and here forms, as the basal portion of the caput, the grey substance above the lamina perforata anterior (fig. 238, *L*). Gratiolet designates this mass the *olfactory area*. I may be allowed to confirm anew the application of this term, by showing that the basal substance of the corpus striatum is invested by a thin layer of the cortex, the continuity of which, with the cortex of the olfactory lobe, may be easily demonstrated in the prolongation of the neuroglia and

of the nerve-cell layer. This layer coalesces posteriorly with the hook convolution. Its presence exhibits the uniform applicability of a law of formation by virtue of which the whole surface of the vesicles of the hemispheres is covered with cortical substance, and by which, consequently, also the septum pellucidum comes to be classified among the cortical substances. The coalescence of the temporal extremity of the cauda with the temporal process descending from the third segment of the lenticular nucleus (pedunculus nuclei lenticularis) occurs close behind the amygdaloid nucleus. The substance of the caput of the corpus striatum, folded around it like a gutter, invests the external (ventricular) surface of the septum pellucidum at the height of about eight millimeters, forming the nucleus septi pellucidi (fig. 241, *J*).

The tissue of the substance of the corpus striatum is composed of a delicately punctated connective tissue, like that of the cortex of the cerebrum, with similar apparently free nuclei sparingly distributed through it. The nerve corpuscles of the corpus striatum are of two sizes. Some are large, with many processes, and attain a diameter of 30 μ, whilst others, and these are by far the most numerous, are small, being only 15 μ in length, but are also multipolar. It is probable that part of these cells form cells of origin for the spinal cord, whilst others are cells of origin for the fibres of the cerebellum; and for the following reason. The mass of the crusta of the cerebral peduncle, which is continued into the pyramids of the medulla oblongata, is at least three times the size of the latter; and this diminution is due to the turning aside, within the pons, of fibres of the crus cerebri into the fasciculi of the crura cerebelli of the pons through the agency of grey substance.

There cannot, consequently, be any doubt that the ganglia of origin of the crusta of the cerebral peduncle are also centres of origin for the fibres of the cerebellum. A motor function must therefore be attributed to the cerebellum even from this morphological point of view alone. For no other view can be taken, than that the impulses conveyed from the cortex to the corpus striatum and the lenticular nucleus, besides their conduction into the spinal cord, at the same give rise to definite modes of activity of the cerebellum.

The small but unquestionable nerve corpuscles referred to must not be confounded with elements appearing like free nuclei which Luys (in the corpus striatum) regards as nerve corpuscles connected with the fibres of the cerebellum that pass through medullary fasciculi of the crus cerebri into its grey matter. These chains of apparent nuclei, parallel to the fasciculi, are simply the nodal points of the reticulum of connective tissue in the medulla,—a common character of the latter.

The first link of the projection system presents four forms of connection with the corpus striatum.

1. Radiating fasciculi proceeding from the whole length of the arch of the hemisphere.

2. An arcuate fasciculus from the cortex of the apex of the temporal lobe, which, running along the internal border of the corpus striatum, penetrates into the most anterior region of its caput, as the stria cornea.

3. Connecting fibres between the cortex of the olfactory lobe and the corpus striatum, consisting partly of superficial fibres proceeding from the bulb, and partly of deep fibres from the medulla of the olfactory lobe (fig. 238, *m'*). Those portions of the medulla of the olfactory lobe that pass into the anterior commissure appear to traverse the substance of the corpus striatum in an uninterrupted manner. The medullary fibres of the olfactory lobe pass also through the nucleus septi pellucidi in the form of arcuate fasciculi.

4. The cortical substance of the septum is likewise connected with the basal mass of the corpus striatum, by means of the pedunculus septi.

The basal region of the caput of the corpus striatum exhibits, from above the lamina perforata anterior to near the height of the passage of the anterior commissure, a structure differing from that of the remaining portion of the corpus striatum. This still awaits a monographical exposition, but it may be here stated that it presents two remarkable characters—(1) a close aggregation of small forms of nerve corpuscles into circumscribed nuclear-like structures, and (2) the presence of extremely small granules (6 μ in diameter), which are nowhere else to be found in the cerebral ganglia, and which, aggregated into dense clusters, lend to this region, traversed by the me-

dulla of the olfactory lobe, a textural similarity to the structure of the latter. This difference in structure, both as regards the arrangement and form of the elements, appears to indicate an independent functional endowment of the grey mass, which is thus fused with the nucleus caudatus.

The origin of the crus cerebri, from the caudate nucleus, is effected very simply by its fasciculi emanating from the concavity of the arch, converging towards the base of the brain, and uniting into the crusta of the peduncle (fig. 238, *P*).

Speaking generally (with the special exception of the stria cornea), the *external* and at the same time *superior* border of the nucleus caudatus represents the cerebral pole, which receives the corona radiata, whilst the *internal* and *inferior* border constitutes its peripherical pole, which gives off the cerebral peduncle.

The fasciculi of the crus cerebri, proceeding from the nucleus caudatus, traverse the upper layers of the internal capsule (figs. 244, 245, *Ci*), in order to reach its basal region. This broad and, when seen in horizontal section, obtuse-angled medullary tract (fig. 243, *m Th*, *P*) runs forwards between the nucleus caudatus and lenticularis, and backwards between the latter and the thalamus opticus. The upper half of its layers belongs to the first link of the projection system, namely, the pes of the corona radiata; the lower, to the second link of the projection system, that is, the pes, or crusta, of the crus cerebri. The pes of the corona radiata is, however, covered in the internal capsule by the nucleus caudatus, and is therefore traversed and decussated by the peduncular fasciculi of the latter, as is shown in the radiations (in fig. 238, *Th*) running from the frontal lobes, and entering the optic thalami.

Certain fasciculi proceeding from the caudate nucleus into the crus cerebri, pursue a more complicated course. After removal of the tractus opticus, fasciculi appear running transversely to it, which crop up between the external fasciculi of the crus cerebri, and again disappear between the inner ones.

These are fasciculi descending from the more externally situated tail of the corpus striatum, which complete their course towards the spinal cord in the internal region of the transverse section of the crus cerebri, and therefore make

their way superficially over the intermediate fasciculi. They are clearly to be distinguished from the subsequently described loops of the crus cerebri, which only partially interweave with the crus cerebri of their own side, and never bilaterally.

The *lenticular nucleus*, or corpus striatum externum (figs. 233, 242, 243, 244, 245), which is the second ganglion of origin of the crusta of the cerebral peduncle, is perfectly identical in its textural structure with the intra-ventricular portion of the corpus striatum. The two different-sized forms of nerve corpuscles occur in it, but still no region of aberrant structure is found in it resembling that of the basal portion of the caudate nucleus, which is traversed by the fasciculi of the olfactory lobes. The ganglion is wedge-shaped. The base of the wedge is directed towards the frontal portion of the brain, and towards the insula, whilst the apex is prolonged into and continues with the crusta of the cerebral peduncle; it presents a slender, dentated, sigmoid, curved border. In sections made transversely through its substance (figs. 242, 243, 245), the first glance shows the presence of two systems of fasciculi running in different directions, one arranged radially upon the base of the wedge, the other concentrically with the surface of the wedge, and descending from the internal capsule to the base of the brain. The last-mentioned fasciculi form concentric dissepiments of the *laminæ medullares*, which break up the lenticular nucleus, as a rule, into *three* segments, of which the internal is applied to the origin of the crus cerebri, whilst the external is separated from the claustrum belonging to the cortex of the insula by the thin medullary lamina of the external capsule (figs. 244, 245, *Ce*, and also in figs. 242, 243). The latter, connected by means of loose cellular tissue, simply lies on the lenticular nucleus, without having any medullary connection with it. A few thin and inconstant medullary fibres of the external capsule, which cut through the superficial portions of the third segment of the lenticular nucleus, form an exception to this statement.

The two internal segments of the lenticular nucleus are distinguished from the third segment, which is the largest of the three, as the globus pallidus, on account of the

large quantity of medullary fibres traversing them. This arises from the fact that the third segment is traversed only by fasciculi originating in itself, and has a larger quantity of grey matter (since it is the base of the cone), whilst the internal

Fig. 245.

Fig. 245. Transparent transverse section from the region of the Insula and of the principal ganglionic masses (from the brain of Man, slightly enlarged). *J J'*, cortex and medulla of the Insula ; *Cl*, claustrum, with clumps of transition-formations between the base of the claustrum and the amygdaloid nucleus ; *V*, the grey matter of the third ventricle ; L_1 L_2 L_3, the lenticular nucleus ; *N C*, the caudate nucleus ; *B*, the basal portion of the caudate nucleus ; *V C*, anterior commissure ; *J K*, region of the internal peduncle (Stiel), and, *a K*, region of the upper peduncle of the optic thalamus ; *M*, pes of the corona radiata (Stabkranzes) ; *Ce*, external capsule ; *Ci*, internal capsule ; *Schl*, *L*, *St*, *Z*, the four layers of the substantia innominata, or of the loops of the crus cerebri ; *G*, descending crus of the fornix ; *A*, commissure in the central grey substance of the ventricle ; II, optic nerve, with the optic basal ganglion lying upon it.

segments, in addition to those fibres which originate in themselves, are traversed by the fasciculi of the third segment on their way to the crus cerebri. Just as the caudate nucleus

pushes forth its thin extremity to near the apex of the temporal lobe, so also does the lenticular nucleus extend a small temporal process (pedunculus nuclei lenticularis) to the temporal lobe of the cerebrum in order to receive from it medullary radiations. This process starts from the opposite end of the nucleus to that which is turned towards the frontal lobe.

The region which in transverse section (fig. 245) appears as the upper border of the lenticular nucleus is its centric pole; for the fasciculi of the corona radiata here penetrate from the internal capsule into the lenticular nucleus.

The region appearing in transverse sections as the lower border of the lenticular nucleus and its internal extremity represents its peripheric pole, from which a large portion of the crusta of the cerebral peduncle proceeds. The form of the lenticular nucleus necessitates that the radiations directed inwards from the cortex of the frontal and parietal lobes must be incomparably greater than those from the occipital and temporal lobes. Independently, however, of the quantitative distribution of the fibres, the connection of the lenticular nucleus with the cortex of the cerebrum must be considered to be universal. The walls of the Sylvian fissure (including the insula) also send projection-fasciculi into these ganglia. This, however, is not effected radially by means of the convex portion of the third segment which is in apposition to the island, but by curving fasciculi which wrap round the upper angle of the lenticular nucleus, proceeding from the medulla of the insula into the internal capsule, and enter the lenticular nucleus as its most external fasciculi. If we consider the first and second links of the projection fasciculi connected with this ganglion (independently of the interrupting nodal points of the ganglion cells) as a continuous mass, the projection tracts by no means pursue the shortest course radially through the lenticular nucleus, but they describe complex spirals which are composed of concentric segments with their surface turned downwards, and of radial segments with their surface turned inwards. All radially running middle and inferior fasciculi, as, for example, those in the third segment of the lenticular nucleus, enter this part in sectional planes situated further forwards, beginning with the upper border of its transverse

section, and descend parallel to its external convex surface before they assume a radial course inwards towards the crusta of the cerebral peduncle. As the sum of the fasciculi *towards the interior* increases by aggregation in proportion to the length in transverse section of the line of contact of the receiving superior border with the medulla of the hemispheres, which sinks to zero at the external extremity of this border, so do these concentric tracts which within the third *segment* are microscopic, here form coarse, distinctly visible lines, the *medullary septa* (laminæ medullares), between the *segments* which by the addition of nerve corpuscles, and by decussation with the radial tracts by which they are traversed, form complex ganglionic plexuses.

The number of large nerve corpuscles is here very remarkable, and the position of their long axes is obviously parallel to the direction of the concentric fasciculi. In the pale clumps (globus pallidus) of the lenticular nucleus, the arrangement of the nervous elements is very close, and the amount of intermediate amorphous connective tissue is very small. A portion of the fasciculi taking part in the formation of the laminæ medullares does not traverse in its further course one or both of the internal segments of the lenticular nucleus, but runs at the basal surface of this nucleus directly into the peduncular stratum of the internal capsule. These fasciculi form the innermost area in transverse sections of the crusta, and consequently pass not only over the inferior surface of its ganglion, but also over the external and median fasciculi of the crusta itself, in the form of a transverse sling or loop nearly parallel to the tractus opticus, forming the loop, collar, or fillet of the crus cerebri (figs. 245 and 247, *Schl*). This constitutes the deepest stratum of the ansa peduncularis of Gratiolet, described at p. 427, or of the substantia innominata of Reil. The haste of these fasciculi to reach over the others from the most external ganglia of origin towards the median line is explained by their being destined to attain elevated points of decussation.

The innermost fasciculi of the crusta terminate peripherically in the central grey substance of the ventricle within the nates (superior pair of the corpora quadrigemina) as they there penetrate into the nucleus common to the oculo-motor and

trochlearis nerves, after an antecedent decussation analogous to the decussation of the pyramids of the spinal cord. We may therefore suppose that the loop or collar of the crus for the most part embraces the lenticular ganglion of origin for the *motor cranial nerves.*

In frontal transverse sections carried, as in fig. 248, through the posterior extremity of the third ventricle, the area of the transverse section of the crusta has become, not only complete in its fascicular mass proceeding from the caudate and the lenticular nuclei, but it has also associated with itself the fascicular mass coming directly from the cortex of the occipital and temporal lobes, which as the most external fasciculi of the crusta become invested by the tractus opticus, the pulvinar, and the corpora geniculata, and therefore enter the transverse section of the crus cerebri (fig. 243) immediately in front of these masses. During its descent through the region of the mesocephalon, however, a fresh addition to the crusta is made from the third of its ganglia of origin, the grey matter of Soemmering (figs. 248, 249, *S*). This superficially expanded ganglion forms the boundary between the crusta and the tegmentum of the crus cerebri, and is continuous centrally with a thin fan-like corona radiata, which terminates in it. Peripherically fasciculi originate therefrom (fig. 248), which traverse the internal and middle regions of the transverse section of the crus cerebri, forming a clear plexus dividing it into small areas. This includes in part individuals of the large form of pigmented cell, to the presence of which the ganglion owes its name of substantia nigra, and in part cells of very small size. The external part of the crus, springing directly from the cortex, obtains no accession of fibres from the substantia nigra.

Thus, upon the whole, there are four territories of origin for the crusta of the cerebral peduncle: 1. The *cortex* of the occipital and temporal lobes of the cerebrum; 2. The *nucleus caudatus* (corpus striatum internum); 3. The *nucleus lenticularis* (corpus striatum externum); and 4. The *substantia nigra.* The parts taking origin from these centres are so distributed over the transverse section of the crusta that the most external area proceeds from the cortex of the cerebrum, and the innermost from the lenticular nucleus, whilst the intermediately placed

and widest tract is common to the caudate and lenticular nuclei. The substance of Soemmering participates merely in the formation of the middle and internal area proceeding from the ganglia.

The sizes of the cerebral lobes and of the crusta of the cerebral peduncle, with its ganglia, rise and fall together in the brains of different Mammals, proportionally to one another. If, for example, the cerebral lobes in Man, the Baboons, and the Roe-deer amount respectively to 78, 70·8, and 62 per cent. of the whole brain, the ganglia of the crus (insula, with the corpus striatum internum and externum) form in the same series 58, 40, and 33·3 per cent. of all the structures composing the cerebral peduncle, and the size of the crusta to that of the tegmentum in Man is as 1 : 1; in the Baboons as 1 : 3; and in the Roe-deer, as 1 : 5. Moreover the preponderance in the case of the lenticular nucleus in Man is far larger than in the case of the nucleus caudatus, which is dependent upon the circumstance that the latter is only continuous with what is in Man an atrophied portion of the hemispheres—the olfactory lobes.

The Tegmentum and its Ganglia.

The variations presented by the ganglionic region of the posterior tract of origin of the spinal cord show that its size is independent of the development of the lobes of the cerebrum. In the brain of Man, indeed, the relative size of this region is remarkably diminished in comparison with that of Mammals. For example, in Man the optic thalami form 19 per cent.; in Monkeys, 30 per cent.; in the Roe-deer, 22·9 per cent. of the entire mass of the sensory ganglia: whilst the corpora quadrigemina in Man amount to 6·5 per cent.; in Monkeys, to 10 per cent.; and in the Roe-deer, to 16·6 per cent. of the same group of organs.

The chief ganglia of origin of the tegmentum are—(1) the *optic thalami* and (2) the *corpora quadrigemina*. Besides the common feature of serving as centres of origin for the spinal cord, these ganglia are also alike in their connection with the tractus opticus. The latter feature they share with the *corpora geniculata*, which must doubtless be regarded as an appendage to the above-named ganglionic system. Further

forwards the fasciculi of the spinal cord belonging to the tegmentum are developed (3) from the *corpus mammillare;* (4) from a *ganglion* interposed amongst the *loops of the crus cerebri;* and (5) from the *pineal gland.*

The *thalamus opticus* (Sehhügel), sharply separated by the medullary investment of its zonular layer from the grey substance of the nucleus caudatus, appears at first sight to project as an uncovered ganglionic mass from the wall of the third ventricle. This grey matter of the ventricle, however, is only to be regarded as a layer of tissue foreign to that of the optic thalamus proper, and to belong, as the lining of the primary anterior cerebral vesicle, together with its prolongation into the tuber cinereum, the infundibulum, and the posterior segment of the pituitary body, to the central grey substance of the ventricles. Luschka describes the pituitary body as atrophied grey substance, containing much connective tissue, like the atrophied lower extremity of the central grey substance in the filum terminale. The anterior division of the pituitary body, however, must certainly be classed as a foreign and only juxtaposed formation, altogether external to the nervous system. By Henle it was regarded as a structure allied to the medullary portion of the suprarenal bodies, but by Ecker it was placed among the blood-glands, consisting, as it does, of a framework of connective tissue with vesicles containing cells from 30 to 90 μ in diameter.

The *grey matter* of the *cavity of the third ventricle* still awaits a monographic description. The following structures may, however, be provisionally regarded as present:—

At the lateral margin of the tuber cinereum is the *basal optic ganglion,* which is about 1·5 millimeter in breadth, and is composed of fusiform ganglion cells, having a long diameter of 30 μ, and a short of 15 μ. It commences above the chiasma, and stretches, having a length of more than one centimeter, immediately above the tractus to the posterior margin of the tuber cinereum. With Luys I include this optic basal ganglion in the substance of the tuber cinereum, because, together with this, it extends downwards in the grey terminal plate over the surface of the lamina perforata anterior, of which J. Wagner regards it as a part, and reaches farther backwards

than the latter. Still, like the tractus itself, it follows the inner margin of the lamina.

In sagittal sections (fig. 247, II') the ganglion presents the form of a sickle with the concavity forwards. Luys states that the ganglia of opposite sides come into contact in the median line, which I have not observed to occur, and thinks the roots of the optic nerves arising in them decussate in the tuber cinereum, which is certainly incorrect, since the fine medullated fasciculi (and not as Foville maintains, grey roots,) immediately turn outwards into the nervus opticus. The specimens that show most clearly that there are non-decussating optic fasciculi may therefore be obtained from this region of their origin. Appreciating fully the difficulties of settling this question from sections, I do not feel myself qualified, in regard to the remaining portion of the nervus opticus, either to deny the complete decussation stated by Biesiadecki to exist in the chiasma, nor, from the results of my own examinations, altogether to coincide with his view.

The fact of the existence of a connection between the optic nerve and the central grey substance of the ventricles by no means justifies its comparison with the peripheric nerves that arise from the latter. In place of maintaining that there is an analogy between its chiasma and the chiasma of the olfactory nerves, and between the retina and the olfactory bulb, and of regarding the optic fibres as a peripheric link of the projection system (a view directly contradicted by the character of these fibres, which are fine, non-medullated, and like those of the central white substance of the brain), it is more reasonable to regard the root in question as an upper link of the projection system, and to see its central extremity in the grey concentric substance of the retina, which is allied to the cortex of the cerebrum, and its peripheric extremity in the *basal optic ganglion*, from which presumably tracts that are still unknown, running in the central grey matter of the ventricle, extend to some peripheric organ—perhaps to the musculature of the eye.

2. Immediately behind the basal optic ganglion the tuber cinereum includes a *commissure* (fig. 245, *A*), the fasciculi of which turn backwards within the central grey substance of the ventricle, though their ultimate destination is still unknown.

3. Without being connected with the substance of the optic thalami, the *posterior longitudinal fasciculus* of the *tegmentum* of the crus cerebri runs along the grey substance of the central cavities—first, of the third ventricle, and subsequently of the aquæduct and fourth ventricle (figs. 245—253, *L*). The central extremity of this fasciculus lies in a flat expanded ganglion (fig. 245, *L*), beneath the fillet or loop of the crus cerebri belonging to the lenticular nucleus (collar of the crus), corresponding to the second stratum of the substantia innominata of Reil, or *anse pédonculaire* of Gratiolet, a mass which stretches above the optic tract transversely over the crusta (fig. 245, *Schl*, *Z*). The cells of this ganglion extend into the external capsule, the converging fasciculi of which (so far as their medulla does not consist of connecting systems) spring from the cortex of the upper edge of the fissure of Sylvius (Klappdeckel), and terminate, not in the lenticular nucleus, which they only cover, but in the *ganglion* of the peduncular loop or collar of the crus (fillet). Occasionally a few fasciculi, either alone or mingled with some interspersed fusiform cells (50 μ long and 15 μ broad), traverse the superficial strata of the third segment of the lenticular nucleus. Besides its origin from the upper edge of the fissure of Sylvius, the upper link of the projection system for this ganglion also arises from the remaining walls of the Sylvian fossa, from its medullary portions, which, proceeding from the cortex of the insula, and from the temporal lobes, traverse the claustrum. Fibrils from the lowermost parts of the infundibulum also attach themselves to the inferior longitudinal fasciculus, covering the pillars of the fornix internally, whilst the greater part of the longitudinal fasciculus lies external to the pillars of the fornix.

4. Another mass of the grey substance of the central cavities included in the optic thalamus is constituted by the descending pillar of the fornix, as well as by the commencement of the ascending, before this penetrates into the ganglionic mass of the optic thalamus (fig. 246, *Fd*, *Fa*).

According to Meckel, Arnold, Jung, and Luys, the descending crus of the fornix, before its entrance into this grey substance, fuses with the anterior extremity of the stria cornea (but surely not with the whole!) and with that of the brachia

of the pineal gland. The upper hemisphere of the *corpus albicans* (fig. 246, *M*) is imbedded with the roots of the fornix in the basal mass of the grey substance of the central cavities.

The corpus albicans or mammillare is a ganglion that is included in a loop of the fornix, by which the passage of a part of its fasciculi into the tegmentum is effected. The statement made by Jung, that the fasciculi of the fornix only traverse the substance of the corpus albicans, and that its medullary investment is derived from another source, is quite erroneous. On the contrary, the descending crus of the fornix forms the medulla of the external and posterior surface of this ganglion, and, passing into the ascending crus, winds round to its internal and anterior surface.

By this means a portion of its fasciculi passes through the ganglion, which consists of fusiform cells having a long diameter of 20—30 μ, and a short of 9 μ, and from the upper border of which (fig. 246, *m*) the fasciculus for the crus cerebri enters into the tegmentum. The greater part of the fasciculus, however, only touches the ganglion, and contains, especially in the ascending root of the fornix, closely arranged parallel nerve corpuscles with a long diameter of 30—45 μ, and a short of 15 μ, which appear to agree in size with the terminal cells of the ascending crus in the anterior tubercle of the optic thalamus (fig. 247, *G*, *Tu*). The peripheric extremities of the fasciculi of the fornix are therefore connected with two forms of terminal cells, of which the smaller lie in medullary corpuscles, the larger in the course of the crus and the anterior tubercle of the optic thalamus.

The shape of the optic thalamus would be completely misunderstood if we included the above-described grey substance of the central cavities in its mass; for it would then appear as though the anterior extremity of the optic thalamus extended down to the base of the cerebrum, whilst it really lies quite remote from it. For the anterior extremity, the lowermost region of the transverse section of the optic thalamus, rests not only upon the crus cerebri, but also upon the wedge (in transverse section) of the lenticular nucleus (fig. 245, *a K*, L_1, L_2, L_3). But still Burdach's description, that "inferiorly they are seated like a pair of capitate processes on the crura cerebri,"

is not sufficiently accurate and precise. The essential form of the optic thalamus is (with various modifications of the division of its mass) that of an arch moulded around a transverse axis, which is the fundamental form also of the lobes of the cerebrum as a whole, and is like that which is characteristic of the nucleus caudatus amongst the ganglionic masses. Just as the lenticular nucleus forms the axis of revolution for the latter arch, so do the transverse ganglionic masses form the axes of revolution for the optic thalamus, partly directly, partly by their transverse processes extending into the medulla of the hemispheres. These axes of revolution of the thalamus are the brachia of the superior and inferior corpora quadrigemina (fig. 243, *Q*, *Bs*, *Bi*), as well as the *internal* corpora geniculata moulded around the inferior brachia of the corpora quadrigemina (fig. 243, *Gi*). The mass of the optic thalamus developed in front of the axis of revolution (fig. 243, *Th*) is the longest, whilst the portion lying behind this axis, the so-called pulvinar, or cushion (fig. 243, *P*), is by far the shortest.

The thalamus opticus attains its greatest breadth in the pulvinar, and its greatest vertical diameter in front of the axis of revolution, whilst both dimensions are smallest at the anterior extremity.

There is only a partial justification for admitting the existence within this general form of special nuclei in the interior of the optic thalami; for the whole of the grey matter of the optic thalamus forms a continuous mass, and no characteristic differences in its textural composition have hitherto been satisfactorily demonstrated. The presence of more or less completely detached nuclei in the optic thalamus is merely dependent upon the *mode of radiation* of the *upper links* of the *projection system*, as well as, on the other hand, upon the mode of origin of the *crus cerebri* in the *optic thalamus;* so that with the knowledge of the two latter the knowledge of the former is necessarily associated.

The upper *link* of the *projection system* proceeds from the frontal lobes, from the walls of the Sylvian fissure, and from the temporal lobes to the anterior extremity of the optic thalamus, in *four* forms of radiation. In three directions the substance of the optic thalamus forms obtuse prolongations

meeting these radiations, which are connected with the penetrating white substance as with peduncles.

1. The *anterior peduncle* of the optic thalamus proceeding from the frontal lobe between the corpus striatum and lenticular nucleus penetrates straight into the anterior extremity of the optic thalamus, by which means it helps to form the *internal capsule* of the lenticular nucleus (figs. 243, 238, *m th*). In the substance of the optic thalamus this compact medulla breaks up in a brush-like manner (fig. 238), so that the longitudinal section of the thalamus appears obtusely conical anteriorly. The most superficial portion of the brush-like radiation assists, before it enters the grey mass, in the formation of the stratum zonale. 2. The *inferior peduncle* of the anterior mass of the optic thalamus proceeds to this from the substantia innominata, and likewise forms a radiating brush (figs. 245 and 247, *Sta, K I K*), and the continuity of its fasciculi may be especially followed for a long distance backwards in the internal region of the optic thalamus. It forms the third stratum of the ansa peduncularis, or collar of the crus (fig. 245). Its region of origin is the cortex of the Sylvian fossa and of the temporal lobe. 3. This stratum of the loop of the crus cerebri is still covered by a fourth (fig. 245, *Z*), which penetrates indirectly into the optic thalamus, inasmuch as it joins the fasciculi of the *stratum zonale* which describe a series of spirals around the surface of the grey substance of the optic thalamus before entering its more superficial layers. The *substantia innominata* of Reil may consequently be divided into four layers, each pursuing a different course—(1) a layer forming the loop of the lenticular nucleus, which belongs to the crusta of the cerebral peduncle; (2) a layer forming the ganglion of the loop of the crus cerebri with the origin of the posterior longitudinal fasciculus; (3) the inferior peduncle of the optic thalamus; and (4) the anterior temporal portion of the stratum zonale. Each fasciculus of the ansa peduncularis is composed of two segments, of which the more central is seen in frontal transverse sections as a tract running in a general way parallel to the tractus opticus (fig. 245), whilst the more peripheric portion is brought into view by sagittal longitudinal sections (fig. 247), and presents, immediately above the tractus opticus, the incipient divergence of its

fasciculi in accordance with the various peripheric termini to which they pass. 4. The fourth converging series of fasciculi, entering the anterior extremity of the optic thalamus, is composed of fibres coming from the cortex of the gyrus fornicatus, thus forming the ascending pillar of the fornix, which constitutes an *upper peduncle* of the optic thalamus (fig. 247, *G*). After it has completed a slightly sigmoid flexure, first

Fig. 246.

Fig. 246. Transparent sagittal section of the Thalamus opticus of Man, near its internal surface. *Th*, Thalamus opticus ; *Qu*, corpora quadrigemina ; *Z*, the pineal gland ; *H*, the ganglion of the peduncle of the pineal gland (Zirbelstile) ; *M*, corpus mammillare ; *T*, tuber cinereum ; *R*, red nucleus of the tegmentum ; *S*, substantia nigra ; *A*, wall of the aquæductus Sylvii ; *II*, chiasma nervi optici ; *C*, anterior commissure ; *III*, nervus oculomotorius ; *Sz*, stratum zonale ; *J*, fasciculi in the interior of the substance of the optic thalamus from the inferior peduncle ; *Fd*, descending crus of the fornix ; *Fa*, ascending crus of the fornix ; *P*, posterior commissure ; *L*, posterior longitudinal fasciculus ; *m*, fasciculus passing to the tegmentum from the corpus mammillare.

curving inward away from the posterior longitudinal fasciculi, and subsequently while in the substance of the optic thalamus, turning somewhat outwards, it passes straight forward and upward, and, after dividing in a forked manner, as is brought into view by a frontal section, enters the *upper nucleus* of the *optic thalamus*, its anterior extremity being apparent on the outer surface as the tuberculum or genu anterius (fig. 247, *Ta*). The

tuberculum, however, is only the head of a kind of nucleus caudatus in the optic thalamus, in the shape of the upper nucleus, which, turned backward and outward, is prolonged into a tail which terminates in the pulvinari. This is the most nearly, though certainly not completely, isolated nucleus of the optic thalamus, inasmuch as the zonular layer splits as it were into two layers that surround it, defining its limits clearly both in longitudinal and transverse sections. Its most anterior part, however, coalesces, without any line of demarcation, with the internal substance of the optic thalamus.

The internal capsule conveys radiations from the posterior portions of the *frontal* and *parietal lobes*, not only to the anterior extremity of the optic thalamus, but also to the middle of its length. The transverse section of the optic thalamus and that of the lenticular nucleus form the two corresponding diagonal halves of a square applied to the *internal capsule*. And just as the upper surface (in section the upper border) of the lenticular nucleus was its *recipient* territory, so is it the obliquely sloping *inferior surface* of the optic thalamus along which the contact and connection with the internal capsule occurs.

It would be hazardous to maintain that the middle portion of the optic thalamus is connected exclusively with the parietal lobes. For, independently of the long course of the fasciculi of the *anterior peduncle* of the *optic thalamus* proceeding from the frontal portion of the cerebrum, as well as of the *inferior*, running backward from the temporal lobes, the temporal lobes participate to a remarkable extent in the interpenetration of the most externally situated region of the grey matter of the optic thalamus. Projection fasciculi of this cerebral lobe here occur, running in an arched manner from behind forwards into the optic thalamus, and decussate with the radially converging fasciculi (as, for instance, with those proceeding from the parietal lobes) to form a web which is the *trellis-work* of the optic thalamus. This interweaving of fibres occurs, that is to say, not in the medulla of the hemispheres, but in the most external layers of the optic thalamus itself, so that a thin stratum of its substance still remains as a claustrum of the optic thalamus, external to the interrupted medullary capsule of its trellis-work, in the fasciculi

of which it is imbedded (fig. 243, between *Th* and *P*). The first representation of a converging system of radii from the internal capsule into the optic thalamus in sections of the cerebrum was made by Kölliker, whose histological illustration of the structure

Fig. 247.

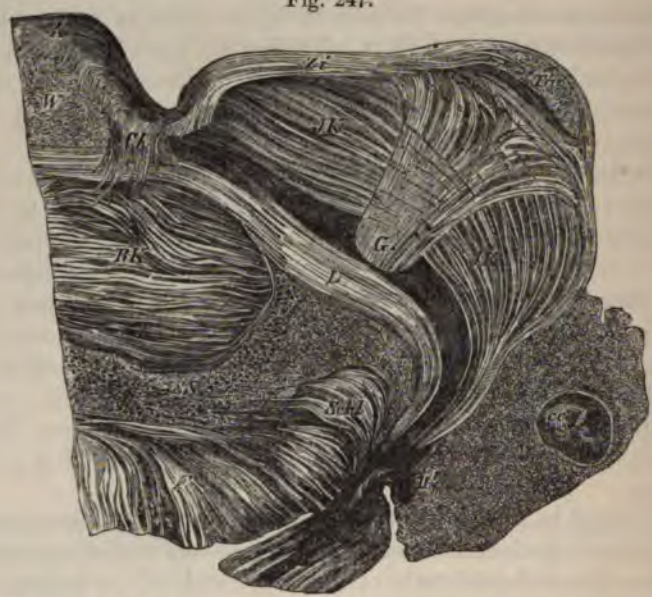

Fig. 247. Transparent sagittal section through the anterior tubercle of the optic thalamus of Man. *Ta*, Tuberculum anterius; *JK*, internal layer of the optic thalamus; *K*, corpora quadrigemina; *W*, wall of the aquæductus Sylvii; *RK*, red nucleus of the tegmentum; *SS*, substantia nigra; *F*, pes of the crus cerebri (crusta); II, tractus opticus; II′, basal ganglion of the optic nerve; *Zi*, stratum zonale; *c c*, anterior commissure; *Ch*, posterior commissure curving downwards to the tegmentum of the crus cerebri; *G*, ascending crus of the fornix; *Jk*, *L*, *Schl*, three converging fasciculi, which coalesce to form the loop of the crus cerebri—*Jk*, inferior peduncle of the optic thalamus; *L*, the posterior longitudinal fasciculus; *Schl*, the loop of the pes cerebri proceeding from the lenticular nucleus.

of the brain, in regard to its microscopic anatomy, combines rare knowledge of the organ with accurate microscopical detail.

The posterior region of that part of the optic thalamus which still lies in the third ventricle, and consequently anterior

to the pulvinar, is bounded by the whole breadth of the medulla of the cerebrum, since at this part, in consequence of the lenticular nucleus not extending so far, the inner capsule is no longer defined. The substance of the optic thalamus here exhibits a *superior* and an *inferior* layer, which are separated from one another by an intervening dentation seen on section of the white substance (fig. 248, at II*R*). The *upper* and *lower layers* of the optic thalamus completely coalesce, as regards their grey matter, and are traversed throughout their entire height (fig. 248, *Th*), as far as to the innermost lamina medullaris (*T'*), to be hereafter described, by a uniform series of radiating fasciculi, which alternate with layers of equally thick grey substance in which they terminate.

The cells of the substance of the optic thalamus, both in its upper and lower layers, have an average length of 30 μ, and breadth of 10 μ, and are fusiform, with their long axes always arranged parallel to the radiating fasciculi. These uniform fasciculi which enter the confluent upper and lower layers of the optic thalamus arise however from two different centres. Those of the *upper layer* apparently arise exclusively from the *medulla of the cerebral lobes*, and thus from the *cortex* of the *cerebrum*, whilst those of the *lower layer* proceed from the tractus opticus, and consequently from the *retina*, forming the yet to be described *middle root* of the tractus opticus. This enters into the substance of the optic thalamus between the external corpus geniculatum (fig. 248, *c*) and the crusta of the cerebral peduncle (*P*), proceeding from the medulla of the tractus (about twelve millimeters in front of the posterior border of the pulvinar). This general similarity of its connection with the optic thalamus to that of the cortex of the cerebrum appears to lend to the retina characters permitting it to be associated as a centre with the cerebral cortex itself; whilst, on the other hand, the hereafter to be described completely distinct mode of origin in the optic thalamus of the peripherically distributed tracts of the crus cerebri, indicates a not less noteworthy difference between the tractus opticus and peripheric nerves, and between the retina and the terminal organs. The affinity here noted between the mode of convergence of the fasciculi from the cortex of the cerebrum and the retina into the optic thalamus is

rendered complete by the fact established by Arnold, of the connection of the optic tract with the zonular layer of the optic

Fig. 248.

Fig. 248. Transparent vertical transverse section of the thalamus opticus and crus cerebri at the posterior boundary of the third ventricle. *M*, The medulla of the hemispheres; *Th*, the thalamus opticus; *V*₃, the third ventricle, lined by the central grey matter belonging to the internal surface of the optic thalamus; *H*, the ganglion in the peduncle of the pineal gland; *Cm*, the centrum medianum of Luys; *C*, corpus geniculatum externum; *Nc*, nucleus caudatus; *TT*, the tegmentum of the crus cerebri; *RK*, the red nucleus of the tegmentum, the medullary fasciculi of which issue from the medulla of the hemispheres between II*R* and *S*; *P*, the pes of the crus cerebri; *S*, the substantia nigra; *II*, tractus opticus; *Sz*, stratum zonale; *R*, the radiating fasciculi in the optic thalamus entering its upper layer from the medulla of the hemispheres; II *R*, the radiating fasciculi in the optic thalamus which penetrate its inferior layer from the tractus opticus; *T'*, the concentric laminæ medullares for the tegmentum of the crus cerebri; *H'*, the fasciculus from the ganglion of the peduncle of the pineal gland for the tegmentum; *L*, transverse section of the posterior longitudinal fasciculus.

thalamus, which is otherwise exclusively composed of the upper link of the projection system.

The connections of the posterior region of the optic thalamus with the occipital and temporal lobes have already been discussed at p. 409.

The origin of that portion of the tegmentum which springs from the optic thalamus presents three parts, comprising (1) tegmental fasciculi of the posterior commissure; (2) the laminæ medullares; (3) tegmental fasciculi from the ganglion of the peduncle of the pineal gland. The centre of origin of the latter fasciculi alone (figs. 248, *H*; 241, *I*) is really well defined, appearing as an oblong clavate nucleus at the inner side of the stratum zonale, the superjacent fasciculi of which represent the upper link of its projection system. The large fasciculus (H^1) of the crus cerebri, proceeding from the ganglion of the habenula (peduncle of the pineal gland) bends, covered by the grey matter of the third ventricle, in a sigmoid curve, first outwards towards the posterior longitudinal fasciculus (*L*), then inwards towards the red nucleus of the tegmentum, which it frequently traverses with some of its fasciculi, and arches rectangularly behind the substantia nigra, to run downwards as the most anterior and innermost fasciculus of the tegmentum. Perhaps a decussation occurs in the posterior commissure, between it and the zonular layer of its ganglion.

The ganglion habenulæ is larger in brutes than in Man, and exhibits, in consequence of the close aggregation of cells, a structure differing from that of the remainder of the optic thalamus, and more resembling that of the pineal gland itself.

The region of the two other origins are not separated from one another in the optic thalamus; nevertheless, they constitute two sharply defined formations, which we may conceive to be divided from one another by a line, commencing behind the external border of the tuberculum anterius, and extending to the outer border of the ganglion of the habenula. The inner of these *regions* may be regarded as the *layer* of origin for the *crus cerebri* through the *posterior commissure*, and the outer of these regions as the layer for the origin of the crus cerebri through the laminæ medullares.

The fasciculi from the cerebral lobes which enter the optic thalamus, by its *anterior* and *inferior peduncles* (as in fig. 247, *Jk*) run *longitudinally* through the *internal layer* of the

thalamus, and reach the posterior commissure; but this course, on account of the curves which it describes inwards, is not seen in section-specimens, though it may be easily demonstrated by separating the fibres. The fasciculi alternate very regularly with layers of grey matter, of equal thickness with themselves, in the cells of which, elongated in the same direction as the fibres, and having a long diameter of 30 μ, and a breadth of 10 μ, they terminate as fasciculi of the cerebral hemispheres, and arise as fasciculi of the crus cerebri. For after the fasciculi of the posterior commissure have extended about five millimeters beyond the median line, they enter the anterior part of the tegmentum of the crus (fig. 247, *Ch*), within which they descend as fasciculi of origin of the spinal cord.

The posterior and *external* layer of the optic thalamus presents a superficial resemblance to the internal structure of the lenticular nucleus, as in both the *medulla* of the *hemispheres*, extending radially to its terminal cells, is crossed by concentrically arranged medullary lamellæ, which are roots of origin of the crus cerebri that arise from these ganglia. Of these concentric lamellæ in the interior of the thalamus (fig. 248, *T*), only the innermost, named *lamina medullaris* by Burdach, and forming the boundary between the imaginary external and internal nucleus of the optic thalamus, has been noticed by authors. But, inasmuch as the lamina medullaris is confined (almost exactly) to the posterior half of the optic thalamus, the separation of these nuclei ceases at all events in the anterior half of the optic thalamus. Luys remarks, on the other hand, that this layer of medulla invests in the centre of the optic thalamus a nucleus which is sharply defined posteriorly superiorly, below and to the outer side—the "*Centre median*" (fig. 248, *Cm*). The cells of which this centre is composed do not differ in form and size from those of the remainder of the optic thalamus. Its radiations, belonging to the corona radiata, proceed from the anterior peduncle of the optic thalamus. The lamina medullaris, however, which bounds the *internal nucleus* of Burdach, and the "*Centre median*" of Luys, is not really an independent structure, but only the innermost of a number of concentric medullary laminæ, through which, in opposition to the crossed tegmental origin in the posterior commissure, direct roots of

origin of the crus cerebri proceed from the optic thalamus. The relation of these fasciculi of the crus cerebri and spinal cord which furthermore surround the cerebellar portion of the transverse section of the tegmentum, the *red nucleus* (fig. 248, *Rk* in *T*), to the radiation of the optic thalamus coming from the retina (fig. 248, II*R*) is exactly the same as their relation to the radiations proceeding from the cortex of the cerebrum (fig. 248, *R*) to the optic thalamus.

If we suppose the anterior part (fig 245) of the optic thalamus to be immediately seated upon the commencing crusta of the cerebral peduncle forming the internal capsule, two fan-like sets of fasciculi from the corona radiata are interposed in the inferiorly situated segments between the substance of the optic thalamus and the crusta. The upper of these fans, by the convergence of its fasciculi, presents a round area on transverse section, which becomes the central point of organization of each half of the tegmentum of the crus cerebri, and, on account of its containing between its fasciculi a large number of very small nerve corpuscles, swells up into a ganglionic mass, which receives the name of *red nucleus* of the tegmentum (figs. 246, 247, 248, and 249, *Rk*). This red nucleus is the first internode of a tract that originates with the above-mentioned fan of the corona radiata in the cortex of the cerebrum, and, on the other hand, stretches to the cortex of the cerebellum. The *processus a cerebello ad cerebrum* are a free segment of this connecting tract between the two cortical substances.

The second more slender fan of the corona radiata, which lies beneath the former, is applied to the substance of Soemmering, which sends a pointed process outwards to meet it, the relation of which to the crusta of the cerebral peduncle has already been described. Thus the optic thalamus (fig. 248) rests upon the whole mass of the crus cerebri, of which the crusta at this level already appears in sections as a completely formed structure; the tegmentum, however, so far as regards its spinal-cord portion, being first met with in a completed state in sections made through the region of the corpora quadrigemina.

In the corpora quadrigemina there is found a second connection common to them with the optic thalamus and the corpora

geniculata, namely, that with the tractus opticus. This relation of the corpora quadrigemina is given here in anticipation of a further description of them, because, for one thing, the consideration of the optic thalamus, as well as generally of those ganglia of the cerebrum which terminate in the region of the crus cerebri, will thus be completely finished, whilst the corpora quadrigemina constitute a boundary region belonging to the pons, which will be considered in our next section.

In the planes of *origin of*, or rather of *convergence of fibres* from the *tractus opticus*, the posterior extremities of the optic thalami, the pulvinaria, by their divergence, retreat from the median portion of the territory of the crus cerebri, allowing the corpora quadrigemina to press in between them. In place of lying upon the latter, the pulvinar lies upon the two corpora geniculata (fig. 249, *Th*, *Gi*, *Ge*), and the stratum zonale sends its fasciculi towards the tractus opticus, by means of which it partly arises from the retina, and partly from the medulla of the temporal lobe, in an arch parallel to the tractus, and destined for quite identical regions of the optic thalamus. There are thus two connections of the tract with the optic thalamus: (1) a *superficial* one, that has just been mentioned; and (2) a *deep-seated* one, already described on p. 431.

The external corpus geniculatum presents in transverse section a plump heart-shaped, and consequently bilobed form, which is not quite distinctly enough expressed in fig. 249, *Ge*. J. Wagner must have taken one of these lobes for a special structure when he enigmatically speaks of a well-defined optic nucleus in the optic thalamus, which he, in his drawing, confuses with the lamination of alternate grey and white substance peculiar to the external corpus geniculatum. The grey matter of the external corpus geniculatum is not a rounded mass, like that of the ganglia, but a lamina, which however, as if for the purpose of its being included in a complete medullary capsule, is folded in a zigzag manner, as is shown by successful longitudinal sections. If we recall the laminated optic nerve of fishes, which is likewise folded upon itself in its sheath, we may explain the structure of the external corpus geniculatum morphologically as follows: A lamina of grey matter lies between two medullary laminæ, of

Fig. 249.

Fig. 249. Transparent transverse section from the ganglia of origin of the optic tract of Man. *M*, The medulla of the cerebral lobes ; II, the tractus opticus ; *Rk*, red nucleus of the tegmentum ; *Nc*, nucleus caudatus; *St*, stria cornea; *Th*, pulvinar; *Qu*, superior corpus quadrigeminum; *Gi*, corpus geniculatum internum; *Ge*, corpus geniculatum externum ; *S*, substantia nigra; *A*, aquæductus ; *A'*, grey matter of the central cavities around the aquæduct; *R*, the median raphé of the tegmentum ; *La*, lamina perforata posterior ; *R'*, converging radiations into the pulvinar ; *Bs*, the brachium of the upper corpus quadrigeminum ; *Bi*, the brachium of the inferior corpus quadrigeminum, from which the lowermost fasciculi of the internal corpus geniculatum run into the tractus opticus ; *W*, optic root of the upper corpus quadrigeminum (through the intermediation of the internal corpus geniculatum) ; *Xp*, decussation in the roof of the aquæduct, through which the right arm of the superior corpus quadrigeminum is conducted into the loop layer of the tegmentum, *Tl* ; *Xd*, decussation in front of the aquæduct, which is part of the interlacement of the tegmentum, *To*, formed by fibres proceeding from the fifth nerve, *V* ; III', roots of the oculo-motor nerve ; *T*, spinal-cord fasciculi of the tegmentum ; *V*, transverse section of the descending root of the fifth with the adjoining vesicular cells ; *L*, posterior longitudinal fasciculi; III, nucleus of the nervi oculomotorius and trochlearis ; *P'*, fasciculi of the crus cerebri entering the above-named nucleus as the fibræ rectæ of the raphé, *R*.

which one is a portion of the medulla of the tractus, the other of the medulla of the hemispheres. At their adjoining surfaces the medullary laminæ connect themselves with the cells of the grey laminæ, whilst they, like the enclosed grey substance, are folded in a zigzag manner. In this manner grey and white laminæ alternate continuously with each other, as is apparent in every section of the external corpus geniculatum. The cells of this ganglion are from 30 to 48 μ in length, and 15 μ in breadth, and are for the most part coarsely granular and pigmented. The mass of the tractus belonging to the external corpus geniculatum lying internally to the superficial origin of the optic thalamus, and externally to the deep, is very large (fig. 249, II).

The connections of the external (and internal) corpus geniculatum with the occipital (fig. 243) and temporal lobes of the cerebrum have already been given at page 409.

Situated internally, and in great part also anteriorly, to these external fasciculi of the tractus is the connection of the latter with the oval or fusiform internal corpus geniculatum, by which the fasciculi of the tract traversing it in a meridianal direction, and proceeding from its fusiform cells (the long diameter of which amounts to 25 μ, and their breadth to 5 μ), are conducted in reduced number in the form of an *upper* and a *lower* band to the corpora quadrigemina. The *superior* or indirect connection of the tractus opticus with the nates passes below and somewhat behind the arm of the nates, in a brush-like manner, into the small cells of this body (fig. 249, *Gi, W*).

An *inferior* connection with the corpora quadrigemina is effected by the internal corpus geniculatum in such a manner that fasciculi traceable from the tractus opticus are conducted to the brachia of the *testis*, and consequently to this ganglion itself. No more striking argument in respect to the significance of the optic nerve, and in opposition to its being regarded as a peripheric nerve root, can be adduced than this attachment of one of its fasciculi to the brachium of the inferior corpus quadrigeminum, which is nothing else than a fasciculus of the corona radiata arising in the cortex of the cerebrum, and terminating in the ganglion of the inferior corpus quadrigeminum (fig. 249, *Gi, Bi*).

The *internal corpora geniculata* in Mammals keep pace with the development of the two pairs of corpora quadrigemina with which they are connected. The internal corpus geniculatum develops in harmony with the size of the tegmentum, not alone on account of its relation to the corpora quadrigemina, but because it attaches itself, especially by its fasciculi associated with the arm of the inferior corpus quadrigeminum, to the ganglia of origin of the tegmentum, which relation, however, requires further elucidation.

The most internal fasciculi of the tractus opticus encircle partly the crusta of the crus cerebri, and partly interweave with its most external fasciculi (fig. 248). I am unacquainted with their ultimate distribution. I can only with certainty refer to the illusory appearance which, on a superficial examination, makes it appear that these tracts connect themselves, as Burdach has stated, with the closely adjoining substantia nigra. They really always cease abruptly near or behind it.

The *region of the corpora quadrigemina* is situated internally to the so-called origin of the optic nerve, forming a coalesced mass of three stages, superimposed upon one another around an excentric cavity situated at a high level, which is the aquæductus Sylvii (fig. 249, *A*). The corpora quadrigemina extend over the aquæduct, their central portion constituting its roof. Immediately anterior to the aquæduct lie the tegmenta of the crura cerebri, fusing in the middle line in a raphé (*R*), the under surface of which forms the lamina perforata posterior (*La*). Laterally on each side of the latter extends the transverse section of the most inferior stage of the quadrigeminal region, viz., the crusta. The *corpora quadrigemina* are composed of a *superior* and *inferior* pair of ganglia, that together, and with their brachia (which are the fasciculi of the corona radiata entering them from the cortex), occupy a transverse position in the cerebrum. This, however, is not strictly correct in regard to the inferior brachia, because these are pressed forwards as axes of revolution by the cushion of the optic thalamus (fig. 243, *Bi*). The ganglia of the corpora quadrigemina lie imbedded between a superficial (fig. 249, *Bs—Xp*) and a deep medullary layer (figs. 249, *Xp—Te*; 241, *m'*). The superficial represents a kind of *zonular layer*, resembling

that of the optic thalamus, and is formed by the unfolding of the brachia of the corpora quadrigemina, and is the only fasciculus of the first link of the projection system that is freely exposed on the surface of the cerebrum. The deep medullary layer represents the origin of the tegmentum of the crus cerebri. The two systems of medullary fibres decussate with one another, and are therefore fused at the middle line. The deep layer loses its compactness in its posterior fifth, in consequence of its finer distribution through the grey matter of the ganglion, and is no longer distinguishable as a special medullary layer (fig. 250, *Q*). From the substance of the bodies a processus corporis quadrigemini ad cerebellum is developed on either side (probably as a continuation of the decussating fasciculi of the brachia), a name which however by no means belongs to what usually bears it, the (so-named) superjacent superior peduncle of the cerebellum, but only to the frenulum, which is distinctly composed of two opposite halves that pass through the valve of Vieussens to expand in the superior vermiform process of the cerebellar medulla.

The transverse section of the median medulla of the corpora quadrigemina is identical with the medulla of the posterior commissure (fig. 241, *m'*). The latter, however, proceeds not only from the centre of origin, already mentioned, in the optic thalamus, but is also continuous with the ganglion named the pineal gland (conarium) and with the ganglion of its habenula. The whole of this structure appears in longitudinal sections of the cerebrum (fig. 241, *m'*, *Z*, *Z'*) as an S-shaped appendage of the median medulla of the corpora quadrigemina, which is composed (1) of a series of sections, in the form of an inferior groove open posteriorly, constituting the *posterior commissure;* (2) of a superior groove placed upon this, and open anteriorly, constituting the second curve of the S, the *pineal gland*, with its medullary fasciculi arching parallel to the surface; and (3) of a beak of the S divided into two symmetrical sections, the *ganglion* of the *peduncle of the pineal gland*, forming with its longitudinal fasciculi, which, according to Arnold, Jung, Luys, Inzani, and Lemoigne, are continuous also with the fornix, the boundary between the optic thalamus and the grey matter of the third ventricle. The symmetrical

division of the peduncle of the pineal gland extends in the fœtus of Man, and as a persistent condition in the adult state of many Mammals, through the centre of the pineal gland itself (Luys).

The presence of true commissural fibres of the posterior commissure is also admitted by Burdach and Arnold.

The *pineal gland* has often, but very incorrectly, been compared with the Hypophysis cerebri. Luys still continues to regard it as a continuation of the grey matter of the middle ventricle. According to the more accurate statement of Arnold, however, it is separated from the latter by its medulla. It is to be regarded as a ganglion which, similarly constituted to that of the peduncle of the gland, is, like the latter, continuous on the one hand with the medulla of the hemispheres, and on the other, by means of the posterior commissure, with the crus cerebri. It may consequently be considered a *ganglion of origin* of the *tegmentum*. It is composed of two forms of cells, one of which has a diameter of 15 μ, whilst the other is much smaller, and does not exceed 6 μ; in structure it is distinguished from other cerebral ganglia only by the close aggregation of its cells. In the peduncle of the pineal gland the dense rows of cells alternate regularly with medullary layers, and frequently exhibit an appearance similar to the granule and medullary layers of the bulbus olfactorius. The admixture of these medullary layers, and the constant presence of processes from the cells, compel us to regard the latter as nerve corpuscles. Their close arrangement is common to them and to the stratum corporum arctorum of the cornu Ammonis, and this with their minute size is common to the olfactory lobes, the cortex of the cerebellum, and certain accumulations in the grey substance of the corpora striata. The latter however contains, in addition, dense masses of larger nerve corpuscles.

The convergence of the fasciculi of the projection system proceeding from the cortex of the cerebrum to the corpora quadrigemina is effected through the brachia of the nates (fig. 249, *Bs*) and the brachia of the testes (figs. 249, *Bi*; 250, *B**). The brachium of the nates traverses the thalamus just above the corpus geniculatum, in consequence of which a triangular region of the transverse section of the optic thalamus is in-

closed between it and the corpus geniculatum (fig. 249, *Bs*, *Ge*, *Gi*).

The brachia of the corpora quadrigemina terminate, perhaps like all the remaining fasciculi of the corona radiata, in the ganglion of the hemisphere of their own side. The median decussation lies on the other side of their interruption by means of the cells of the corpora quadrigemina, and belongs to the fasciculi of the crus cerebri after their origin from the mass of the corpora quadrigemina.

No doubt can exist respecting these relations of the brachia of the corpora quadrigemina so far as regards the deeper-lying fasciculi directly penetrating the ganglion substance; but we may also with certainty make the same assertion as to the fasciculi of the brachia that in the first place help to form the medullary investment of the corpora quadrigemina, because the cells of the nates and testes not only belong to the grey matter of the nuclei, but are freely interspersed also through the most external layers of the zonular layer, so that these fasciculi of the corona radiata are by no means obliged to penetrate into the interior of the opposite nucleus in order to reach their terminal cells. The relation of the most anterior fasciculi of the brachia of the nates to the decussation is less obvious; for these in transverse sections of the brains of Monkeys perforate the thalamus opticus in very loose arrangement, whilst in traversing the nates they form a very compact fasciculus. Nevertheless it is probable that the above-named, and still to be more minutely described, fasciculi terminate in the ganglion of the corpora quadrigemina of the same side, inasmuch as they curve round to the middle line, and may run backwards in order then first to decussate. The course of the fasciculi finely distributed through the grey substance which in longitudinal sections may be seen running through the superior pair of the corpora quadrigemina, and which extend from the entrance of the brachia of the nates to points situated far behind in the median decussation, is in accordance with this supposition (fig. 241, *Q'*).

It has already been stated that fasciculi from the tractus opticus are associated with the brachium of the inferior pair of the corpora quadrigemina whilst it is invested by the internal corpora geniculata.

The *grey matter* in the interior of the *corpora quadrigemina*, like that on the internal surface of the optic thalamus, belongs to the grey matter of the central cavities; as the grey matter surrounding the aquæductus, it forms the continuation of the lining of the third ventricle. The description of this grey matter, which is to be distinguished from the ganglia of the corpora quadrigemina, must first be given, because its presence and its intimate connection with the former renders the significance of the corpora quadrigemina in one respect extremely clear. The central grey substance of the cavities around the aquæductus Sylvii is limited posteriorly by the decussation of the medulla of the corpora quadrigemina, and anteriorly by the transverse section of the posterior longitudinal fasciculi (figs. 249, 250 *A'*, *Xp*, *B*×, *L*). Its transverse section in the upper pair of the corpora quadrigemina is surrounded laterally by sharply defined marginal fibres that run into the tegmentum, whilst in transverse sections of the inferior pair of the corpora quadrigemina its limits are not less sharply defined by a chain of transverse sectional areas of fasciculi gradually developed in the wall of the aquæduct itself, and external to the posterior longitudinal fasciculi; these are the descending roots of the fifth nerve (fig. 250, 5'). The various forms presented at different heights by the transverse section of the aquæduct with its lining of columnar epithelium have been described by Gerlach. If by means of a transverse line passing in the nates in front of, and in the testes through, the aquæduct, the ring of central grey substance surrounding it be divided into two semi-circles, the cells distributed through the posterior semi-circle will be found to be small, having a long diameter of only 25 μ and a breadth of 5 μ, whilst those in the anterior portion of the section are larger, having a length of 30—50 μ and a breadth of 15—25 μ. The larger cells are in part more sparsely scattered, but in part also form a compact mass; as the latter they constitute, in the neighbourhood of the nates, bounded by fibres, which will be immediately described, the *oculo-motor and trochlear nerve nucleus*, strictly so called, which lies behind the posterior longitudinal fasciculi, and is lodged in an excavation in the upper half of the testis. In a wider sense belong also to the same nucleus the scattered formations which are

inferiorly indistinguishable from the similar cells of the eminentia teres.

The *nucleus* common to the *oculomotorius* and *trochlearis* nerves is in connection (1) with straight fibres of the raphé (fig. 249, III, *P'*), which, in so far as they are not already connected with precisely similar cells distributed through the raphé itself, spread out with their innermost fasciculi in the scattered masses of the above-named nucleus, and penetrate with their middle and external fasciculi into its compact portion. They thus form finely fasciculated curves, convex internally, to which the internal and somewhat smaller nerve corpuscles of the nucleus are completely parallel. Between this peripheric termination of these fibræ rectæ and their centric origin is an acute-angled decussation. These fibres arise from the lenticular nucleus as the innermost fasciculus of the crusta belonging to the deep stratum of the ansa peduncularis. They constitute for the common nucleus of the third and fourth nerves that which the decussating fasciculi of the pyramids are for the nuclei of origin of the anterior roots of the spinal cord. They are therefore the shortest fasciculi of the system of the crus cerebri, because, having arisen from the lenticular nucleus, they at once penetrate into the most elevated of the motor-nerve nuclei, and here peripherically terminate in the grey matter of the central cavities.

2. From the nuclear mass common to the third and fourth nerves in which these fasciculi terminate, the roots of the third or oculomotorius nerve arise (fig. 249, III') in the form of large bundles that run forwards through the tegmentum on the inner side of the crusta, curving outwards as if they were a continuation of the course of the fibræ rectæ; they partly traverse the red nucleus of the tegmentum, and in part are situated to its inner side. If it be borne in mind that certain fasciculi of the corona radiata terminating in the lenticular nucleus, represent the *upper link* of a *projection tract*, of which the *second link*, arising from this nucleus and running its course in the crusta, passes as decussating fibræ rectæ of the raphé into the nucleus of the oculomotorius, and the *third link* of which is found in the third nerve, this easily com-

prehended segmentation forms a scheme for the course of all the projection masses which course through the anterior tract of the crus cerebri, that is, its crusta, to the entire series of motor nerve roots.

The size of the fasciculi, and consequently the number of fibres these afferent fasciculi of the crus cerebri contain, as well as the calibre of the fibres themselves, is far smaller than that of the emerging roots. These facts, therefore, obviously support the frequently verified statement of Deiters, to the effect that with the interruption of the fibres that takes place in a central nucleus, a change in their nature also occurs.

3. The roots of the *fourth nerve* arise from the same nucleus. The place of decussation of this pair of nerves lies, as Stilling demonstrated, not to the central side of the nuclei of origin, but results from the interweaving of the root fasciculi in the velum medullare (Valve of Vieussens), immediately before their emergence below the corpora quadrigemina (fig. 251, 4).

The representation of the trochlearis and the oculomotorius by decussating fibræ rectæ in the crus cerebri cannot therefore be common to both nerves, unless we admit a recrossing which is certainly not well established from a physiological point of view. The trochlearis roots, which are spread in a brush-like manner, arise chiefly from that somewhat deeper-lying compact region of the common nucleus which lies in an excavation of the posterior longitudinal fasciculi. In transverse sections made through the upper half of the testes, they form marginal fasciculi running round the nucleus posteriorly. In transverse sections through the lower half they appear as compact masses cut across at the ends of the transverse diameters of fibres surrounding the wall of the aquæductus (fig. 250, 4).

The entire tract of the trochlearis, the nucleus of origin of which lies *in front of* the aqueduct and in the vicinity of the nates, and whose point of emergence is behind the aqueduct and *below* the testes, must necessarily encircle the aquæductus Sylvii in a plane sloping from above downwards and also backwards (Stilling). On the other hand, the admission of a second root of origin for the fourth nerve, which Stilling and Deiters have regarded as the so-called inferior tract, rests

upon a confusion with fibres belonging to the descending root of the fifth, which certainly lie very close to the emergence of the trochlearis (fig. 251, 5).

Fig. 250.

Fig. 250. Transparent transverse section from the inferior half of the testes and the uppermost layers of the pons in Man. *A*, The aqueduct, surrounded by the grey substance of the central cavities; *Q*, the ganglion of the testes; *B*×, decussation of the brachia of the testes; *S*, peduncle of the testes (fillet); *m*, upper lamina of the fillet from the nates; *BA*, the connecting arm (processus a cerebello ad cerebrum) decussating with that of the opposite side; *VS*, spinal-cord fasciculi of the posterior division of the pons, situated internally to the connecting arm; 4, transverse section of the root of the fourth nerve; *L*, posterior longitudinal fasciculus; 5, the cells of the substantia ferruginea; 5′, descending roots of the fifth nerve, with vesicular cells of origin; *P*, continuation of the crusta into the anterior division of the pons; *Trp*, deeply situated transverse fasciculi of the brachia of the pons; *Trs*, superficial transverse fasciculi of the brachia of the pons.

The grey substance of the central cavities as high as the nates includes, besides the centre of origin of the *motor* nerve roots in the median line, a *laterally* situated *sensory tract*, to

wit, the *roots* of the *fifth nerve.* These last arise in the most external band of the grey matter around the aquæductus Sylvii, from small clusters of large vesicular cells having a long diameter of 60 μ and a breadth of from 45 to 50 μ (fig. 249, *V*), and form after a time a chain of transverse sections of fasciculi, which, arranged in the form of a flat arch, are applied to the external surface of the thick-walled tube of the aqueduct (figs. 250 and 251, 5′).

We see, therefore, that even at this height a relation exists in the disposition of the motor and sensory masses of origin, which is persistent through the whole grey matter of the

Fig. 251.

Fig. 251. Transparent transverse section of the pons of Man, at the plane of emergence of the fourth pair of nerves. *A*, Central grey matter of the ventricles surrounding the aqæduct; 4, decussation of the fourth nerve in the superior cerebral valve (valve of Vieussens); 4′, transverse section of a fasciculus belonging to the fourth nerve; 5, substantia ferruginea; 5′, chain of the descending roots of the fifth nerve; *L*, posterior longitudinal fasciculus; *BA*, transverse section of the superior peduncle *(processus a cerebello ad cerebrum)* as they pass from the decussation; *VS*, fascicuil of the spinal cord situated internally to the superior cerebellar peduncle; *m*, loop layer from the nates; *s*, loop layer from the testes.

central cavities; the former as a rule occupying a position near the median line, and *in front;* the latter being situated more *laterally,* and at the same time *posteriorly;* their nerves consequently being analogous to the anterior and posterior roots of the spinal nerves.

In the pons and in the medulla oblongata, as Deiters has correctly pointed out, there is a *median lateral* tract belonging to the roots of cerebral nerves, situated between the median and the lateral (posterior) tracts.

The cells from which each fasciculus of the fifth nerve arises, present instructive points of difference from those that are found in the nucleus common to the third and fourth nerves. The former resemble distended vesicles, possess but few and delicate processes that are given off abruptly like a soap-bubble still hanging from a straw. The latter are also large but slender, with numerous processes which gradually become attenuated from their base outwards. The former resemble the cells of the interspinal ganglia, the latter those of the anterior cornua of the spinal cord. The typical forms of the cells of origin of the sensory and motor nerves thus exhibit no striking contrast in regard to their size, though they are characterized by certain well-defined morphological differences.

In Mammals a remarkably distinct dark line extends from the median furrow of the corpora quadrigemina to the upper border of the epithelium of the aquæduct, forming a kind of raphé, which, in the Cat, I have been able to recognize as a median lamina of fibrous connective tissue containing bloodvessels, and which at the posterior margin of the canal divides in a manner exactly similar to the process of connective tissue occupying the posterior fissure of the spinal cord, and towards which extend the fibrillated extremities of the posterior epithelial cells. In Dogs I have seen in this lamella oblong and stellate cells; in Man this dark line is also perceptible, and is most distinct at the level of the testes.

Of the *ganglia* of the *corpora quadrigemina*, that of the anterior pair, or nates, appears in transverse section on each side in the form of a plano-convex lens, the base resting on those fasciculi of the crus cerebri which proceed outwards and forwards from the median decussation; those of the inferior pair, or testes, are delicate bi-convex but sharply defined lenses, the inferior borders of which, again, are circumscribed by the innermost fasciculi of the portion of the crus cerebri proceeding from them.

The nerve cells in the corpora quadrigemina exhibit remarkable variations in size. As a general rule, the smaller forms, having a length of from 15 to 21 μ, and a breadth of 5 μ, predominate, and such are found exclusively in the most super-

ficial layers of both the nates and testes. Nevertheless, in the deeper layers, and more towards the centre of the section, we find (perhaps most abundant in the nates) very large forms, having a length of from 45 to 90 μ, and a breadth of from 10 to 30 μ. These nerve corpuscles lie with their long axes in three directions, so that (1) some are arranged concentrically with the surface, as is particularly obvious in the superficial expansion of the medulla of the arms, *ex. gr.*, along the convexity of the testes; (2) others in considerable number are arranged longitudinally from before backwards, especially along the internal surfaces of the nates, corresponding to the above-mentioned indirect course of the brachia of the nates towards the median decussation (fig. 241, *Q'*). 3. There are also a number arranged in a radial manner around the aquæduct.

A definite arrangement of radiating cells appears to be especially important for the right understanding of the structure of the corpora quadrigemina. We see, particularly with high powers, in transverse sections of the deep medullary layers dividing the grey matter of the ganglia and the grey matter of the central cavities (fig. 241, *m*), that these are traversed radially by fine fibrils. Amongst these fibrils fusiform cells are interspersed, having a length of 45 μ, and a breadth of 10 μ, and the two together constitute a nervous structure connecting the grey matter of the corpora quadrigemina with the grey matter of the aquæductus Sylvii, in which the centres of origin of the nerves for the eye are imbedded. By means of this connection the above-named grey masses appear as a combined and coherent centre, and the morphology thus corresponds to a physiological postulate, demanded as a result of the control exerted by the retina over the ocular muscles. Perhaps just as the fibræ rectæ of the nucleus of the third nerve are the shortest fasciculi of the crusta, we may represent these radiating fibres for the same nucleus as their analogues among the spinal fasciculi of the tegmentum, which may likewise bring the motor-nerve nuclei into connection with the ganglia of origin of the tegmentum.

The *mode of origin* of the *crus cerebri* from the nates and testes is the same for both pairs of ganglia. From

the ganglionic masses which have received the brachia of the corpora quadrigemina fasciculi issue, which, inferiorly to the posterior commissure, form the compact decussating medulla of the middle line. From thence proceeds the indirect prolongation of the *brachium of the nates*, in the form of fine oblique fasciculi, mingled with small elongated (18—25 μ long and 5 μ broad cells, collected anteriorly and externally in a fan-shaped mass which presents a semilunar section, and which is in the first instance covered by the processus a cerebello ad testes, viz., the superior lamina of the fillet (lemniscus) (figs. 249, *Te*; 250, *m*). From the intermixture of cells in this medulla, which already forms a part of the tegmentum, we may conclude that there is an increase in the number of the fibres as it descends.

The *tegmental portion of the testes* passes forwards in the form of fasciculi, which, constituting the *inferior lamina* of the lemniscus, are covered on their external surface by a sickle-shaped portion of the superior lemniscus, in great measure, however, forming the free external surface of the tegmentum. By this means they immediately cover the processus cerebelli ad cerebrum, as it runs outwards from its median decussation at the level of its origin from the corpora quadrigemina (figs. 250 and 251, *m*, *S*, *BA*).

The organization of the tegmentum, which proceeds as a compact mass in the posterior division of the pons (fig. 250), is, properly speaking, still not complete in the lowermost sectional planes of the crus cerebri, but receives an addition in the uppermost planes of the pons. In the corpora quadrigemina, the breadth of the transverse section of the fillet does not quite extend to the raphé, but ceases about five millimeters to its side (fig. 249, *m*). In the uppermost transverse sectional planes of the pons this most anterior fan of fasciculi, supporting as it were the remaining structure of the tegmentum, extends to the raphé (fig. 251, *m*).

This extension inwards, however, is by no means caused by the fasciculi of the most superficial layers of the fillet being thrust inwards, but by an additional formation, which, as Stilling correctly observed, proceeds from the crusta, and occupies the space between the raphé and the layers of the fillet.

Whilst the compact transverse section (fig. 249) of the crusta is broken up (fig. 250) into secondary fasciculi by the penetrating transverse fasciculi of the brachia of the pons, the most posterior transverse fasciculi of the brachia of the pons cut off the hindermost part of the crusta, which in its further course belongs to the tegmentum, forming the innermost portion of the fillet (lemniscus). Notwithstanding that this fasciculus belongs alternately to the crusta and the tegmentum of the crus cerebri, its morphological characters are those of the latter, and it therefore unquestionably belongs to the posterior tract of the cerebral peduncle, since it takes no part in the *decussation of the pyramids*, which is the essential characteristic common to the spinal fasciculi of the crusta.

It thus appears that a still unknown region of ganglia of origin of the crusta must be enumerated with the centres of origin of the tegmentum. These latter ganglia are characterized by the concurrence of both sensory and motor tracts in their interior, a point differentiating them from the ganglia of the crusta, which is of the highest importance to enable us to understand the duplicity of origin of the spinal cord. Within the ganglion of origin of the crusta, however, there is, in point of fact, a region which is connected with a sensorial surface—just as, for example, the optic thalamus is connected with the retina—by converging radii of the olfactory lobe; namely, the *base of the caput of the corpus striatum* above the lamina perforata anterior. This region is at the same time characterized by textural peculiarities resulting from the form and arrangement of the nerve corpuscles, showing it to be a mass which, though fused with the corpus striatum, is by no means homogeneous with it.

The hypothetical reference to this territory of origin of fasciculi of the crusta is perhaps appropriate for the purpose of indicating the direction that should be pursued in a decisive and accurate investigation of the origin of the fasciculi not proceeding from the corpora quadrigemina, that is, of what are called by Reichert the layers of the fillet.

The organization of the *tegmentum* is thus completed at the level at which its inferior ganglia of origin, the corpora quadri-

gemina cease. It consists (1) of the connecting arm (processus cerebelli ad cerebrum) expanded at the level of the nates by the red nucleus of the tegmentum, the cells of which disappear at the level of the testes; (2) of the posterior longitudinal fasciculi springing from the ganglion of the ansa peduncularis (collar of crus); (3) Of a *decussating* origin from the optic thalamus through the tract of the posterior commissure; (4) of a *non-decussating* origin from the optic thalamus, forming the laminæ medullares; (5) of the possibly non-decussating peduncle of the ganglion of the habenula; (6) of decussating fasciculi arising from the pineal gland; (7) of the loop (fillet) from the nates, the upper lamina; (8) of the loop (fillet) from the testes, the lower lamina; (9) of the posterior fasciculi of the crusta.

Before the structure of the tegmentum forms the plexiform region of the processus cerebelli ad pontem, which will be subsequently described, an interweaving occurs in it at the level of the nates, caused by a tract running peripherically into the *large root of the fifth pair*. By this means this segment of the tegmentum, together with certain portions of the fasciculi of the antero-lateral columns, enters into the same morphological relations with the large root of the fifth pair as the medulla obongata does with the posterior roots of the spinal cord, where in it the antero-lateral column is interlaced by the posterior column of the spinal cord. The large cells of origin of the descending roots of the fifth nerve, described at p. 447, which, lying together in clusters, are imbedded in the outermost border of the grey matter of the central cavities around the aquæduct, give origin to a remarkable circle of marginal fibres of the same, which may be collectively termed the *strands of the fifth pair of nerves*. These strands of the fifth are arranged in the form of a thin medullary vesicle (about 150 μ thick), surrounding the aquæduct through almost the entire height of the nates. Somewhat below the transverse diameter of the wall of the aquæduct they become so transposed that instead of being superjacent to one another they lie side by side, and occupy a large space, whilst they diverge from each other like a fountain, and interweave partly with the fasciculi of origin of the spinal cord from the optic thalamus (excluding there-

fore the loop layers) between the posterior longitudinal fasciculi and the red nucleus of the tegmentum, and partly externally to the latter. The first-named tract then obviously passes across the middle line, and, investing the inferior periphery of the red nucleus, may be followed far outwards. Both on the proximal and on the distal side of the decussation, in the adult, there are distributed amongst these *fibræ arcuatæ*, proceeding from the column of the fifth nerve, pigmented nerve corpuscles, having a length of 60 μ, and a breadth of 15 μ, the processes of which form a communication between the origins of the motor columns of the spinal cord and the arcuate fasciculi of the strands of the fifth nerve.

A retrospective glance at the organization of the tegmentum shows that two fundamental differences exist in the structure of its ganglia as compared with the crusta, which are adapted to assist us in determining the significance of these two tracts of origin of the spinal cord.

In the first place, the tegmentum is characterized by the concurrence, on the one hand, of the tractus opticus, and of the origin of (motor) columns of the spinal cord in its grey masses, as well as, upon the other hand, by the communication of the strands of the fifth pair of nerves with these columns through the intermediation of multipolar nerve cells, forming a territory of reflection of centripetal excitation into motion. The ganglia of the crusta, on the other hand, having no connection with sensorial peripheric expansions, point to another source for the excitation of their motor powers; namely, to the conditions of excitation of the cerebral lobes.

In the second place, the nuclei of origin of the tegmentum are centres in which the anatomical arrangement constitutes a mechanism for the production of certain combined movements which can be called into action by the just-mentioned centripetal impulses. This characteristic they obtain from the different origins of the columns of the spinal cord in these ganglia, and especially from their partly decussating and partly non-decussating mode of origin from one and the same ganglion (optic thalamus). As a consequence of this, we may expect that the innervation affecting the ganglion of one side may bring unsymmetrical muscles of the two halves of the body

into the requisite co-ordination for determinate forms of movement. The idea that such mechanisms for co-ordination would betray themselves by anatomical features, has already been advanced by Schröder v. d. Kolk, to whom it was suggested by the appearance of the non-decussating origin of the nervus abducens, as contrasted with the decussating origin of the oculomotorius, to the significance of which we shall hereafter revert.

The fasciculi of each crusta, on the contrary, proceed entirely from the ganglia of their own side, and, as we shall presently show, they have, so far as regards the fasciculi of the spinal cord, a common point of decussation in the course of the pyramids of the medulla oblongata.

The ganglia of the crusta do not therefore appear to be the centres of co-ordination for definite forms of movement, through which, for example, unsymmetrical muscles of the two sides of the body act together. The grouping of the motorial acts must necessarily be already accomplished by the centre that centrifugally innervates the ganglion of the crusta; that is to say, by the cerebral lobes, through the agency of their arched fasciculi acting as a connecting system.

4. The Region of the Interlacement of the Brachia of the Cerebellum with the Projection System.

It would be more correct to precede the description of this region by that of the cerebellum, of that centre which is connected with the projection system essentially by means of transverse interlacing fibres, and by the intervention of grey substance; but I have not done so, because our knowledge of the cerebellum is very faulty, and it will render the subject more intelligible if it be not first considered, but if instead we examine the connections of the cerebellum with other cerebral organs, and thus place one aspect of this organ before our eyes.

The *external form* assumed by this territory of interlacement of the projection system at the base of the brain embraces the surface of the pons and the upper half of the medulla oblongata. Very great differences occur both in re-

gard to the size and apparently also in the nature of the organs seen at the base of the brain in Man and Monkeys on the one hand, and that of almost all Mammals on the other. The aquatic Mammals alone exhibit in this region a formation resembling the more highly developed brains of Monkeys and of Man.

The *variations in size* are referrible to the imperfect development of the pons and of the pyramids of Mammals, as well as to excessive development of the posterior segment of the medulla oblongata, which is the continuation of the tegmentum of the crus cerebri. The *variations in form* are due to the circumstance that in Man the basal surface of the segment of the oblongata in question is marked by three longitudinal elevations: (1) the *pyramids;* (2) the *olivary bodies;* and (3) the *peduncle of the cerebellum,* whilst in Mammals we meet above, near the *pyramids,* with an organ that is apparently absent in Man, the *corpus trapezoides,* forming a thick, plastic, transverse band, extending into the peduncle of the cerebellum, whilst, on the other hand, the corpora olivaria of the human medulla oblongata appear to be deficient.

From this point of view a hybrid kind of formation occurs in the brains of Monkeys (Pavian), inasmuch as the corpus trapezoides and olivary body are both present, though but feebly developed. In the Lemuridæ I found the corpus trapezoides alone.

Nevertheless it is easy to demonstrate that the occurrence or absence of either of these organs is only apparent, and is occasioned only by variations of development. For the corpus trapezoides consists of transverse fasciculi lying behind the pyramids, which in Man are still covered by the longer pons that he possesses, but are exposed in Mammals on account of the narrowness or shortness of their pons; and the lower olivary body can be shown to be present in transverse sections of the medulla oblongata of all Mammals, only it is pressed back behind the pyramids, and does not therefore project externally at their side.

Reflecting on the circumstance *that these variations of form in the medulla oblongata are nothing else than an explicable consequence of the comparative development of the cerebral*

lobes in Man and Mammals, it is impossible to overlook the existence of a widely extended morphological harmony between the form of the highest and of the lowest divisions of the cerebrum.

We obtain the key to this insight into the morphology of these parts from the fact above illustrated, that the crusta of the crus cerebri is directly proportionate in size to the lobes of the cerebrum.

If the size of the crusta be dependent on the size of the hemispheres, and if fasciculi of the crusta pass through the anterior division of the pons into the cerebellum, as appears to occur from the diminution in thickness of this tract in the pyramids, the pons must become correspondingly prominent, the larger the crusta, and *vice versâ*. The pons is therefore prominent in Man, and inconspicuous in Mammals. Since, however, the deeper layers of the transverse fasciculi in the pons of Man are independent of the size of the crusta, these become, if by reason of the small development of the crusta the pons is short, uncovered at a certain height behind and near the pyramids. This is actually the case to a small extent in the brains of Monkeys with feebly developed cerebral lobes, and very completely in the Lemurs. They thus become visible as the *corpus trapezoides in the brains of Mammals*. On the other hand, in Man, the larger prolongation of the crusta, the pyramid, demands space for the increase of its transverse section in the median region of the oblongata, and the *olivary bodies* situated behind the pyramids in the mammalian type consequently become displaced outwards from the median line, and *therefore appear free at the side of the pyramids*.

In addition it may also be remarked that the hemispheres of the cerebellum augment in direct proportion to the cerebral hemispheres, and that a proportionately enlarging ganglion of the cerebellar hemispheres, the *nucleus dentatus*, attains a development of size that keeps pace with that of the inferior olivary bodies. Thus the absolute size of these increases with the development of the cerebral lobes, and their projection from the medulla oblongata augments in the same ratio.

THE CONNECTING ARMS (SUPERIOR PEDUNCLES OF THE CEREBELLUM, OR PROCESSUS E CEREBELLO AD CEREBRUM,) AND THE SUPERIOR MEDULLARY VELUM (VALVE OF VIEUSSENS).

The expression, "interlacement of the projection system through the cerebellum," does not properly exhaust the morphology characteristic of this segment, since in truth a large portion of the fasciculi that pass from the projection system into the brachia of the cerebellum are mingled with it, not only in the pons and superior half of the medulla oblongata, but are already included in the transverse section of the crus cerebri. This primarily refers to the superior peduncle, which was already associated with still higher sections of the projection system, and, as a fasciculus of the corona radiata, even with the medulla of the cerebral lobes, before its fasciculi had become collected together in transverse sections of the red nucleus of the tegmentum.

We are thus here dealing essentially with a separation of the fibres of the superior peduncle from the projection system, and their liberation as an independent mass of fibres extending into the cerebellum, and in consequence of this the fasciculi of this medullary body exhibit the following phases of arrangement:—

Whilst the fasciculi of the superior peduncle are separated in the region of the crus, anterior to the nates, by finely granular grey connective material, containing nerve cells of two different sizes (one having a long diameter of 45 μ, and a short of 15 μ, and the other having a length of 15 μ, and a breadth of 3 μ), so as to form the red nucleus; this peduncle becomes reduced in the lower half of the nates, through the disappearance of the finely granular grey matter, to a pure tract of white fibres that is obviously of smaller size than the red nucleus.

This medullary tract has however only become free from the connective material of the red nucleus; it still contains a large number of nerve corpuscles, and these are still to be found scattered amongst the fasciculi of the superior peduncle in those portions of their course that lead to and from their decussation. But these nerve corpuscles exhibit a remarkable and

peculiar arrangement, inasmuch as they are parallel, not so much to the nerve fasciculi as to the capillaries and finest arterial twigs, to the walls of which they are adherent, arching over the angles of division; and inasmuch also as the long and strong processes of these large nerve corpuscles (45 μ long by 15 μ) run along with and probably within the vascular wall. This character is already demonstrable in the red nucleus, and subsequently on the other side of the point of decussation, the superior peduncle first becoming free from nerve corpuscles below the corpora quadrigemina. Thus, in the central organs, the cerebral capillaries appear to constitute a sort of peripherical surface for the termination of the cell processes, and further research is required to show whether the portion of the superior peduncle included in the crus cerebri be the only field for this kind of relation.

The medullary area of the superior peduncle approaches very closely to the raphé, but never appears as a simple unmixed transverse section, being already at the above-mentioned level, anteriorly to the inferior half of the nates, mingled with a large number of transverse striæ, in which portions of the superior peduncle, seen in transverse section, curve round in order to pass from the right to the left side, and *vice versâ*, decussating with one another. The decussation lies between the posterior longitudinal fasciculi and the layers of the fillet, the remaining fasciculi of the tegmentum for the spinal cord having all been pressed outwards by the connecting arm. Proceeding from the decussation, the fasciculi of the superior peduncle pass outwards as far as to the internal surface of the inferior fasciculi of the fillet (coming from the testes), which consequently form the investment of the decussated superior peduncle.

The more the decussation of the superior peduncle, and the formation of the *crossed* superior peduncle (which occurs in the region of the lower half of the testes, and of the emergence of the trochlearis) is completed (figs. 250 and 251, *A*), by so much the more is the point of decussation concentrated in the anterior half of the back or posterior division of the pons. The superior peduncles of both sides thus form a horse-shoe closed in front, in the posterior opening of which is enclosed

the greater part of those spinal fasciculi of the tegmentum that fill the space between the posterior longitudinal fasciculi and the fillet layer. A slender portion only of them remains anteriorly to the decussation between it and the layers of the fillet. Their disposition in this region is entirely governed by the behaviour of those decussating fibres by which they are interlaced and displaced; being pushed to the outer side so long as the section of the superior peduncle occupies the median line, and again inwards as soon as this obtains a lateral position.

Fig. 252 exhibits a new phase of the course pursued by the superior peduncle. After complete decussation (and it is indeed, as Stilling represents, total, and not as Arnold subsequently maintained, only partial), the superior peduncle elevates itself so as to project freely outwards and upwards from its previous imbedding into the posterior division of the projection system (fig. 252). Above the greatest convexity of the pons it is still covered by a portion which becomes thick in front of the deep-lying lamina of the fillet *S* (fig. 252, on the left side *SA*); it then becomes, opposite the greatest convexity of the pons, completely free, but is already, at the level of the origin of the fifth nerve, imbedded in the medullary mass of the cerebellum (fig. 253, *A*); it is next covered by the other arms of the cerebellum, and beyond this becomes connected with the grey matter of the corpus dentatum.

Whereas it forms in the free part of its course the lateral wall of the fourth ventricle, it is, after its coalescence with the medulla of the cerebellum, only a partial constituent of the extensive medullary roof with which the inferior surface of the cerebellum overarches the grey floor of the rhomboidal fossa (fourth ventricle). In their course between the corpora quadrigemina and the cerebellum, the superior peduncles become complicated by the enclosure of the superior medullary velum, or median valve of the cerebrum (valve of Vieussens, figs. 250, 252, *V*), so as to form, according to the expression of Burdach, the *connecting system* of the cerebellum. This cerebral velum, the continuation of the peduncle of the corpora quadrigemina (frenulum) deserves the name of pro-

cessus cerebelli ad corpus quadrigeminum, which, erroneously, as Arnold showed, has been given to the superior peduncle.

Three kinds of medullary fasciculi interlace in the substance of the valve. 1. The principal mass of its medullary portion consists of the fasciculi of the frenulum. 2. With these principal fasciculi are interwoven above the large decussating fasciculi of the root of the fourth nerve (figs. 251, 4). 3. The valve also includes longitudinal fasciculi from the superior vermiform process which cross the middle line whilst still contained in its substance, and near the posterior border of the testes form a curve with the convexity upwards, in order to run as the posterior fasciculi of the inferior lamina of the fillet, in the back or posterior division of the pons to the spinal cord.

The latter fasciculi of the valve either occur as so frequent an anomaly that Hirschfeld committed no great error in regarding them as the ordinary arrangement in his illustrations of the structure of the brain, or we may consider that (varying considerably in their size) they are really normally present.

As external prominence it will appear that none of the fasciculi of the antero-lateral columns of the spinal cord proceed directly from the cerebellum, though fibres do pass from it to the *posterior* columns; it follows that the innermost or most posterior fasciculi of the deep-lying lamina of the fillet belonging to the valve, in all probability, likewise pass to these latter columns of the cord.

Were we however to regard this formation as a very common anomaly, such a variation of the origin of the *posterior* columns from the cerebellum, in the form of an aberrant loop, at some distance from the other fasciculi, would only constitute an anomaly harmonizing with the general and essential type of structure here met with, whilst even an exceptional passage of fasciculi from the cerebellum into the *antero-lateral* columns would constitute a real deviation from the type. The superior peduncle, moreover, in its way to the cerebellum, is by no means wholly unmingled with other fasciculi, as may be seen on transverse section, being traversed at the level of origin of the fifth pair by the portion of its large root proceeding from the cerebellum (and in part covered by it, figs. 252 and 253, *A'* 5 *d*);

and farther downwards, as will be hereafter mentioned, by fasciculi of the auditory nerve, which even constitute a very considerable portion of its mass.

The Brachia of the Pons (Brückenarme, middle crura, processus e cerebello ad pontem) and the continuation of the Crusta of the Cerebral Peduncle (Hirnschenkelfuss).

The fasciculi of the middle, like those of the superior, crura of the cerebellum are indirectly represented in the projection system of the cerebral hemispheres.

Inasmuch as the fasciculi converging from the cerebral cortex into the lenticular and caudate nuclei are larger than the crusta of the crus cerebri proceeding from them, we must regard all the fasciculi of the latter as an indirect prolongation of the corona radiata, including those that do not reach the spinal cord through the pyramids, but are lost to the projection system in the pons.

Whilst the crusta is broken up by the passage of the transverse fibres of the pons (see figs. 250, 252, 254, *Trs, Tr, O, P*), into secondary fasciculi, these coincidently diminish in diameter in consequence of the bundles which come from the crura cerebri, splitting up still more finely, and part of their fibres becoming connected with terminal cells (30 μ long by 12 μ broad).

These nerve corpuscles, however, occur not only at the borders of the transverse sections of the secondary fasciculi of the crus, where these are obviously in contact and connection with the interlaced fasciculi of the pons, but they are found also (1) within the area of the transverse section of the crus, which seems to show that there is an intimate penetration of pyramidal and pontal fibres in the crusta of the cerebral peduncle, and (2) within the purely transverse fibrous layers on the surface of the pons, and in the deep layers of the anterior division of the pons, where they likewise can only be subservient to the interruption and augmentation of the fasciculi of the cerebellum in some direction.

If, in accordance with the appearances presented by the

transverse section of the pons, the fasciculi of its brachia be divided into (1) a superficial, (2) an interlaced, and (3) a deep-lying portion (figs. 252 and 254, *Trs*, *P*, *Trp*), one is tempted to think that it is the middle series of the transverse fasciculi of the pons only which conduct the interlaced median portions of the fasciculi of the crus to the cerebellum, and the deep-lying stratum in particular seems like some obscure commissural tract belonging to the cerebellum, having no relation to the projection system. Certain considerations, however, compel us to give up the simple conception of more superficial anterior and deeper posterior crossed transverse bands of the crura cerebelli, and to admit that these pursue a more looped course, within which, moreover, the deep-lying transverse layers only represent portions of tracts that are connected by means of cells with the fasciculi of the projection system. The considerations above alluded to are three in number: 1. The deep-lying layer of transverse fibres obviously commences lower down, and ceases higher up, than the superficial strata, on which account hollows (foramina cæca) are formed at the upper and lower edges of the pons over the median fissure of the peduncle. These last without doubt show that the existence of the deep transverse layers depends upon the terminations of the fasciculi of the crus in the cells of the anterior division of the pons, by virtue of which the deep transverse fasciculi are wanting in the uppermost planes, where the transverse sections of the crus have not yet given off any processes (fig. 250), as well as in the lowermost planes, where the transverse sections of the pyramids have already become compact, and the giving off of fibres has ceased; on the other hand, in the centre of the pons, as in the territory of the most extensive termination of the fibres of the crus, they attain their greatest size. 2. We see obviously interlaced fasciculi of one side become fasciculi of the deep layer of transverse fibres of the other side, after curving somewhat posteriorly in the middle line. 3. In all transverse sections fasciculi are found with the deep layer of transverse fibres which wind around the curve of the transverse section of the crus, with their convexity directed outwards (figs. 252, *on the right*, and 254). After they have penetrated hither from the middle line, and therefore

from the opposite middle crus between the longitudinal fasciculi, as interlaced transverse fasciculi, they cross the middle line a second time in the opposite direction, as fasciculi of the deep layers of transverse fibres, in order to pursue a recurrent course in the middle crus from which they were derived. The following theory of the course of the fibres of the pons is the only one that includes the facts above mentioned: Every fasciculus of the middle crus cerebelli crosses the middle line in the superficial layer of transverse fasciculi, then interlaces with the anterior longitudinal fasciculi of the opposite side, becoming connected with them by means of the grey matter. And now encircling them on the outer side, it passes behind the longitudinal fasciculi into the deep layer of transverse fibres, crosses the middle line once more, and runs back again into the cerebellum, through the same middle crus in which it was first contained. If we proceed on this view of the projection system, the course may thus be stated: *that every fasciculus of the cerebral peduncle terminating in the anterior division of the pons is represented by two fasciculi of the opposite middle peduncle of the cerebellum, of which one runs through the superficial, the other through the deep layer of transverse fibres of the pons.* Thus each crusta of the cerebral peduncle is connected with the opposite hemisphere of the cerebellum by the opposite processus e cerebello ad pontem, just as it is connected with the opposite half of the spinal cord by the decussation of the pyramids. Since the crusta of the cerebral peduncle constantly participates in atrophy of the cerebral hemisphere of the same side, this crossed connection of the cerebellum with the cerebral hemispheres may perhaps explain the frequent complication of that atrophy with crossed atrophy of the hemispheres of the cerebellum.

The Inferior Peduncle of the Cerebellum (Kleinhirnschenkel) and the Prolongation of the Tegmentum (Haube).

The pedunculi cerebelli contain the third set of fasciculi that interlace in their transverse course with the longitudinal fasciculi

of the projection system. The relation of the crus or inferior peduncle of the cerebellum (Kleinhirnstiel oder schenkel processus e cerebello ad medullam, restiform body) to the projection system is distinguished from that of the two interlacing systems above mentioned by the circumstance that the *connecting arm* (Bindearm, processus e cerebello ad cerebrum) forms a connection between the cerebral lobes and the cerebellum, which only appears to be interlaced by the projection system; that the *arm of the pons* (Brückenarm, processus e cerebello ad pontem) conducts portions of the second link of the *projection system* into the cerebellum, whilst the *inferior peduncle of the cerebellum* (restiform body) brings an essential addition to the *projection system*, its fibres passing from the *cerebellum* to the *posterior columns* of the spinal cord. The transverse section of the inferior peduncle of the cerebellum breaks up, according to Stilling, into an *external* and an *internal* division. In his great work upon the pons Varolii, so suggestive for cerebral anatomy, he names the *external* division (fig. 257, *M F C*) 'restiform body' (Strickkörper), a large fasciculus, which descends from the cerebellum at the level of the pons between the origin of the uppermost and the lowermost roots of the facial (fig. 254, *Cr*; fig. 255, *St*). The corpus trapezoides of Mammals, and the stratum zonale, which covers the external surface of the medulla oblongata, and especially the inferior olivary bodies, are formed by the breaking up of the fasciculi of its most superficial layers (figs. 257, 258; *Z Z*).

The internal division of the inferior peduncle of the cerebellum emerges from the cerebellum at about the same level of the pons as the corpus restiforme (figs. 254, *ZC*, and 255, *H*), and appears on the inner side of the oval transverse section of the latter as a quadrangular area of fine fasciculi (fig. 257, *S F C*). Stilling is incorrect in describing this internal division of the inferior peduncle as the origin of the slender and cuneate columns. For its fasciculi, apparently descending immediately from the cerebellum (figs. 254 and 255), are far weaker, and, with their small transverse sections imbedded in grey matter containing very large nerve corpuscles (fig. 257, *S F C*), present a structure totally distinct from that of the cuneate and slender columns (fig. 258, *S F C*). It remains separate, and though

diminishing as it descends, is yet still perceptible close to the transverse sections of the latter columns which are distended by the two nuclei they contain, and present a plexiform appearance externally, whilst they are compact internally. If, therefore, Deiters is not justified on the one hand in denying the presence of these fasciculi of the internal division of the inferior peduncle of the cerebellum, which spring directly from the cerebellum, it is possible they may not, on the other hand, quite reach to the posterior column of the spinal cord, but already pass as fibræ arcuatæ into the oblongata above the central canal. At all events, that columnar formation is introduced between them and the corpora restiformia, that enclosing the nuclei which distend it into the form of the cuneate and slender fasciculi, actually passes into the *posterior column*. We shall hereafter show that these last medullary columns, which increase in size as they descend, are the crossed continuation of the corpus restiforme, which are proportionately exhausted.

The inferior peduncle of the cerebellum, which, when superficially examined, appears to be continuous with the posterior column, is composed (1) of the corpus restiforme; (2) of the internal division of the inferior crus cerebelli (Kleinhirnstiel); (3) of the fasciculus cuneatus and the slender fasciculus.

The complete juxtaposition of these occurs at the level of the medulla oblongata, intermediate to the planes depicted in figs. 257 and 258.

The Posterior Transverse Sectional Area of the Projection System.

The description of that interlacement of the projection system which proceeds from the inferior *peduncles of the cerebellum* on both sides, must be preceded by a general view of the mosaic arrangement of the former as it presents itself at various heights.

After this area of transverse section has become free in the uppermost third of the pons from the interlacement of the superior peduncle, where this appears on the external surface of the posterior division of the pons, as the lateral wall of the

Fig. 252.

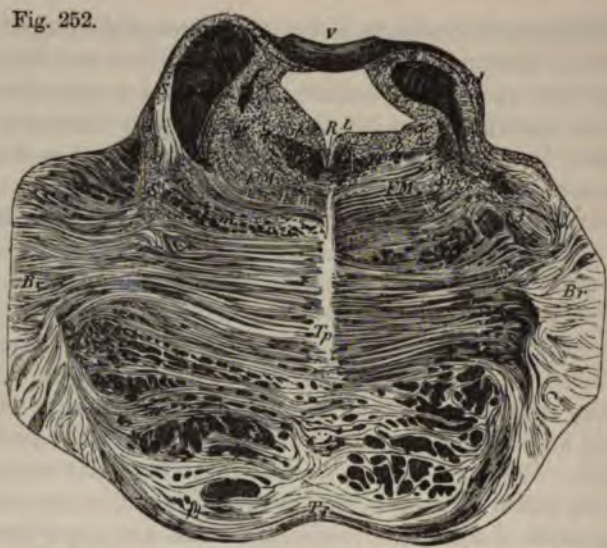

Fig. 252. Transparent transverse section of the pons of Man at the level of its greatest convexity. The left half is made above, the right half through, the plane of origin of the motor root of the fifth pair. *V*, The upper medullary velum (valve of Vieussens), with the little tongue over the fourth ventricle, which becomes enlarged below (consequently on the right side of the figure); *A*, the transverse section of the superior peduncle of the cerebellum in the lateral wall of the fourth ventricle; *L*, the posterior longitudinal fasciculus beneath the floor of the fourth ventricle; *S*, the inferior lamina of the fillet on the left side, still covering the superior peduncle, and on the right presenting a circular transverse section of medullary substance investing the gelatinous substance (*S*); *FM*, the motor area of the posterior division of the pons; *S'*, Reichert's fillet; *Br*, the middle crus, or processus e cerebello ad pontem; *Tp*, its deep; *Ts*, its superficial transverse fasciculi; *P*, the transverse section of the crusta; 5 *m*, the nucleus of origin of the motor roots of the fifth, which run outwards through the arm of the pons (5); *F*, substantia ferruginea anterior; 5 *b*, fasciculi that, proceeding from the substantia ferruginea, traversing and surrounding the posterior longitudinal fasciculi (*L*), pass transversely across the raphé, in order to form on the right side the inner part of the descending roots of the fifth pair externally to the posterior longitudinal fasciculi; with these are associated on the right side, surrounding the inner wall of the posterior longitudinal fasciculus, the fibræ rectæ of the raphé; 5 *c*, the external part of the descending roots of the fifth pair; 5 *d*, portions of the great root of the fifth which are superimposed upon the superior peduncle; *R*, the raphé.

fourth ventricle (fig. 252, *A*), there becomes associated with the portion of the posterior division of the pons, which forms the *tegmental origin* of the antero-lateral columns of the spinal cord (already described), and the crus cerebri, in its further course, the following parts, viz., (1) the transverse section of the portion of the fillet proceeding from the testes, the "*pes of the fillet*" (figs. 252, and 253, *S*); (2) the transverse section of the *ascending root of the fifth* (figs. 253, *Q*; 254, 257, 258, *S*); and (3) the just-described inferior *peduncle of the cerebellum*.

The *tegmental origin* of the antero-lateral column permits distinct areas to be distinguished in two different directions, first those placed one behind the other, which proceeding from the grey floor are (1) the *posterior longitudinal fasciculi*; (2) the (middle) motor area; (3) the fillet (Schleifenschichte, Reichert); and secondly, those in lateral juxtaposition which are (1) the region of the *anterior column*, forming the territory adjacent to the raphé that is bounded laterally in the pons by the roots of the nervus abducens, and in the oblongata by the roots of the hypoglossus; and (2) the region of the *lateral column* extending from this boundary as far as to the ascending roots of the fifth, in which also the *pes* of the *fillet* is enclosed (Fuss der Schleife, Stilling).

The *posterior longitudinal column*, which in transparent longitudinal sections obviously proceeds from the cerebral peduncle, runs continuously through the medulla oblongata, and is prolonged into the posterior fasciculi of the anterior column of the spinal cord; like the *fillet*, it owes its compact appearance and high relief to the large calibre even in the uppermost part of the crus cerebri of its medullary fibres. The remaining area of the continuation of the tegmentum first obtains this compact appearance at a lower point. According to Deiters, the alteration of calibre always first occurs subsequent to or below the point where nerve cells are primarily introduced into the course of the fibres.

The conversion into stronger fibres occurs in such a manner that in the planes of origin of the nervus facialis the portions of the anterior columns adjoining the posterior longitudinal fasciculi and the fillet become progressively more compact; and in the uppermost transverse planes of the medulla oblongata

the whole of the anterior columns appear uniformly dense whilst the lateral columns for the most part do not acquire their homogeneous medullary appearance until as low as about the middle of the medulla.

The *pes of the fillet* proceeding from the testes collects the fasciculi of this medullary fan, so that they present as far as the level of the origin of the facial nerve a nearly annular transverse area (figs. 252 and 253, *S*), which includes a compact mass of cells of such a calibre as may be found even between the fasciculi of the fillet while they still cover the superior peduncle. We cannot agree with Stilling in naming these cells *gelatinous* substance, since they exceed the cells of the latter substance in size, being 30 μ in length and 12 μ in breadth.

From the uppermost planes of origin of the nervus facialis, onward, the pes of the fillet is no longer recognizable by the inclosure of this compact mass of nerve corpuscles, and only contains a few scattered cells distributed through its substance. Still, however, in its further course, it is in no way intermixed, as I formerly supposed, with the transverse section of the ascending roots of the fifth pair (fig. 253, *Q*, on the right side; figs. 254, 257, 258, *S*). Transverse sections of the medulla oblongata, in which the prolongation of the fillet of the testes is exhibited, show, on the contrary, that the pes of the fillet extends as the most external fasciculus of the lateral column into the spinal cord (Stilling), and is applied in the pons and medulla oblongata first to the roots of the facial (fig. 254), and below this point immediately to the transverse section of the ascending roots of the fifth. And whilst the transverse section of this root includes the gelatinous substance continuous with the caput of the posterior cornu of the spinal cord, and loses itself in its cells, the prolongation of the pes of the fillet is applied in the spinal cord to the caput of the posterior cornu. At the inferior extremity of the medulla it may be well seen how the latter exchanges its earlier investment of the roots of the fifth for the lateral and posterior columns which remain in juxtaposition with it throughout the whole length of the spinal cord, because the transverse section of the fine fibres of the fifth always appears, on account of the small quantity of

medulla it contains, in strong relief as a dark area when compared with the white substance of the columns.

The anterior investment of the posterior horn (posterior part of the lateral column) originates in a germ mass, identical with that of the posterior column of the spinal cord, and may be, physiologically speaking, included amongst the centripetal tracts. In the formation of this region, presenting characters that are uniform with the posterior column, perhaps only *those* fasciculi of the pes of the fillet take part that have proceeded through the tract of the valve of Vieussens from the cerebellum (page 459).

In this case the whole of that portion of origin of the fillet layer that, proceeding from the corpora quadrigemina, extends into the spinal cord, would belong to the centrifugal tracts.

Internally to the pes of the loop, and posterior to the layers of the fillet, which leave room for it by a slight convexity of their contour, is found the *superior olivary body* of Schröder v. d. Kolk (figs. 253, 254, 255, 256, *O*), described by Stilling in the brain of Man as an accessory mass of his inferior trigeminal nucleus, but correctly described and named, also in Man, by Deiters. It extends from the uppermost roots of the facial to the lower border of the pons in Man, and in animals to the corpus trapezoides. In the brain of Cercocebus cinomolgus I found it to be two millimeters and a half in length. In Man its outline is insensibly blended with the adjoining parts ; it exhibits in animals, as, for instance, in the Dog, a well-defined contour composed of a sinuous U-shaped external principal mass, and when seen in transverse section an elongated, oval, internal *superior accessory olivary body.* From a longitudinal section of the brain of the Monkey, beautifully made by Dr. Clason, Prosector in Upsala, I am convinced that the superior olivary body is traversed by fasciculi of the continuation of the tegmentum in the posterior division of the pons, which are connected with its slender (30 μ long and 6—9 μ broad) cells, and, as seen in the mosaic presented on transverse section, are found behind the *layer of the fillet* and *internal to the pes of the fillet.*

The *inferior olivary body* belonging to the superior half of the medulla oblongata obtains in Man, by the extension and

close looping of its nucleus dentatus, its highest development, so that Schröder v. d. Kolk erroneously believed the superior and inferior olivary bodies of Mammals to be fused into the lower olive of Man. The so-called accessory olivary bodies (external and internal) agree in being composed of finely granular grey connecting substance and multi-caudate nerve corpuscles, having a length of 24 μ, and a thickness of from 9 to 12 μ, and perhaps constitute masses that are not actually separated from the nucleus dentatus, but are only the external curved border of its lamina, which opens posteriorly and internally in the so-called hilus. The separation of these masses would then be partially simulated by the abundant passage of transverse medullary fasciculi. Reichert, from the macroscopic appearance of the transverse section of the medulla oblongata, maintained the view that the accessory olives are transverse sections of blood coagula in small vessels that have assumed a grey tint in consequence of the action of chromic acid. The inferior olivary body is situated more anteriorly in regard to the longitudinal fasciculi of the tegmentum than the superior, and is imbedded *in the middle of the medulla of the fillet* (olivary column of Burdach), the fasciculi of which, slightly curved inwards and backwards, penetrate the nucleus dentatus in longitudinal spiral lines, join with its cells, and constitute the longitudinal portion of the medulla forming the contents of the olivary sacs. I have completely satisfied myself of this from an examination of Clason's beautiful longitudinal sections of the brain of the Monkey. Deiters has also explained the olivary bodies as being connected with the columns of the spinal cord.

Owing to the conformation of the olivary bodies, such adjoining fasciculi of the fillet as do not penetrate into their interior, but simply cover them, project with a convex surface as "investing columns" ("Hulsenstränge," Burdachs), whose relation to the olives being external, exceptional, and unessential, causes them to be subject to variations in their number and size.

In addition to these detached masses of grey matter, the olives, and to the masses standing in evident connection with the roots of the cerebral nerves, and which will be mentioned further on as their nuclei, the posterior division of the pons

includes in its *motor area* irregularly distributed nerve corpuscles of various calibre, standing in obvious relation to the interweaving of the peduncle of the cerebellum.

The cells of *smaller calibre,* (having a long diameter of 24—33 μ, and a breadth of 9—12 μ,) of the scattered formations, are chiefly found in the pons below the decussation of the superior peduncle of the cerebellum, extending as far as to the planes of origin of the facial nerve (figs. 252, 253, *M F, m*), where they form very numerous small clusters between the transverse sections of the medulla of the *motor area,* whilst they are arranged most closely in the *layers of the fillet.*

In the lower half of the pons these clusters of cells are confined to the transverse section of the fifth nerve, where they are introduced by the transverse fasciculi traversing them, and reappear with these also in the interior of the gelatinous substance as cells of a different size from those that are (there present) characteristic of that part.

Similar clusters reappear also in the lateral columns in the medulla oblongata, viz., in the region of the vagus nerve, on the one hand as a larger division situated to the inner side of the layers of the fillet, forming the *nucleus of the lateral columns* of Stilling, Clarke, and Deiters, and on the other in smaller clusters which are shifted further inwards behind the olivary body.

The cells of larger calibre, having a long diameter of 60 μ, and a breadth of 15 μ, distributed through the motor area, are very sparingly present at that level of the pons where the cells of small calibre are most abundant, but become more numerous at the level of the origin of the facial nerve, and are abundantly distributed, increasing from above downwards, through all this portion of the medulla oblongata.

The large nerve cells, however, are not evenly distributed through all the regions of the transverse section of the above-mentioned length of the medulla. Just as the level at which they appear coincides with the level of the closest approximation of the nuclei of the motor nerves (facialis, abducens oculi, hypoglossus, vagus, and accessorius), so do we find they are most abundant around these nuclei in the vicinity of the grey matter of the floor of the fourth ventricle, and in the lateral

columns. Deiters was therefore justified in stating that, besides the compact nuclei, the scattered clusters of nerve corpuscles stand in a certain relation to the roots of origin of the nerves. I shall hereafter have occasion to recur to this point.

The system of the *fibræ arcuatæ* (indicated in figs. 252—258 by the letters *MFE, MFI, MF,* in *FM, VS,* and by *ar, a, AS, Am*) presents itself at first sight as the characteristic constituent of the tissue of that portion of the posterior tract of the peduncle of the cerebrum which extends from the termination of the decussation of the superior peduncle of the cerebellum to the extremity of the inferior olivary body. The largest number of these *transverse fasciculi* are given off from the *peduncle of the cerebellum,* and participate in the *interlacement* of the *projection system.* The remainder proceed from the nuclei of origin (to be described hereafter) of the roots of the cerebral nerves. The course pursued by the interlaced fasciculi cannot be laid down for all regions, and it is obvious is least evident for planes of section passing through the greatest convexity of the pons, and through the origin of the fifth nerve (figs. 252 and 253) in which the transverse section of the peduncle of the cerebellum is not yet visible, through which it is possible lower down to identify the termini of the fibræ arcuatæ. Let us call this obscure region the

1. First or *superior* interlacement. It is certain that the fibræ arcuatæ are here connected with *clusters* of the small-sized *nerve corpuscles,* and through these with the projection fasciculi (antero-lateral column of the spinal cord). Probably, however, the posterior divisions of these fibræ arcuatæ pass backwards into the cerebellum, internally to the superior peduncle (fig. 252, left side); and on the other hand we may suppose that their extremities are inclined forwards, in order, on the other side of the raphé, to become continuous with the anterior fibræ arcuatæ, which, as will afterwards appear, are always associated with the transverse section of the *corpus restiforme.*

2. The second or *middle interlacement* includes the dentated nucleus of the *superior olivary body,* which, in consequence of the transverse striation produced by medullary substance, acquires a vermiform appearance (figs. 256, 253, 254, 255, *o*).

The transverse fasciculi that proceed in Man from the corpus restiforme at the plane of origin of the nervus facialis immediately behind the deep layer of transverse fibres of the pons, and extend partly in front of, and partly through, the trans-

Fig. 256.

Fig. 256.* Transparent transverse section of the medulla oblongata of Hypsiprimnus murinus, at the level of origin of the auditory nerve. VIII, Auditory nucleus; *P*, pyramid; *MF*, transverse section of the motor area of the posterior division of the medulla oblongata; *R*, raphé; *G'*, gelatinous substance; *O*, superior olivary body; *Kl*, internal division of the peduncle of the cerebellum (processus e cerebello ad medullam, Kleinhirnstiel); *T*, corpus trapezoides; 5, genu of the facial nerve; 6, nervus abducens; 8, root of the auditory nerve; 8', fasciculi from the nucleus of the auditory nerve which are lost in the transverse section of the posterior longitudinal fasciculus, 8''.

verse section of the fifth, so as, after decussating with the *layers of the fillet*, to reach the raphé (fig. 254, *cr* through *S* to *R*) are identical with the fasciculi of the corpus trapezoides (Deiters) which are exposed to view close to the transverse section of the pyramids in animals, on account of the shortness of the pons (figs. 256, *T*, 255, *St*, *Rs*). After decussating in the median raphé of the posterior tract of the cerebral peduncle, they run behind the corpus trapezoides of the other side again outwards, and reach the superior olivary body (fig. 255, *N*—*O*; figs. 254 and 256, *R*—*O*). Through a spiral involution of the surface of this centre they assist in the for-

* Inasmuch as the representation of anatomical systems does not follow planes of section, figs. 256 and 257 are removed from the sequence they would naturally occupy if the successive planes were alone considered; but, in order that the reader may connect the appearances presented by the successive sections, the figures are numbered in accordance with this succession.

mation for it of a medullary capsule (figs. 255, 256, *O*), and enter, by pursuing a transverse course, into its grey substance, with the nerve corpuscles of which they probably unite. Besides this decussating connection with the corpus restiforme, the dentated nucleus of the superior olivary body is also directly connected with the cerebellum by means of fasciculi running straight backwards through the internal division of the peduncle of the cerebellum, which proceed from its capsule, and cannot, on account of their size, be overlooked in animals (fig. 256, *kl*). They are to be regarded as probably forming the continuation of the fasciculi entering the olivary body from the corpus restiforme, and emerging after a complicated course around and through the former.

I cannot suppose that the knowledge of the connections of the superior olivary body has been exhausted in the foregoing account. For we may observe delicate fasciculi, proceeding especially from the neighbourhood of the trapezoid body, and ascending to the external border of the nucleus dentatus superior of the same side, which do not form any link of the chain above described, and cannot be traced with certainty into the restiform body.

3. The third or *inferior interlacement of the peduncle of the cerebellum* includes the *inferior olivary body* (figs. 257, 258). The general relations of its connections are, however, by no means so obvious as those already described of the region of the superior olivary body. I see in it a true measure of the ability of Otto Deiters as an observer, in the circumstance that he penetrated these surprising connections, and that, with certain reservations and modifications, we must acknowledge his views to constitute the key to the right understanding of the structure.

Stilling, Lenhossek, and Schröder, and with still more perfect fidelity Clarke, had indeed described the course of the fibræ arcuatæ in their upper and lower divisions, their connection partly with the external, partly with the internal division of the peduncle of the cerebellum, and their course through the olivary body; but before Deiters no observer imagined that the corpus restiforme, with the anterior divisions of the fibræ arcuatæ and the cuneate and slender columns in the posterior column

of the spinal cord, together with the posterior divisions of this, could constitute portions of one and the same conducting tract continuous with the olivary bodies; and Lenhossek, in admitting the existence of an olivary commissure analogous to the corpus callosum, formed by transverse fasciculi, has laid special stress upon the absence of any relation, for example, between the anterior of these transverse fasciculi and others of the same system.

Fig. 257.

Fig. 257. Transparent transverse section of the medulla oblongata of Man, at the level of the highest roots of the vagus. *VIII* to X^3, the area of transverse section of the grey floor; *P*, pyramid; *O*, inferior olivary body, with (*Z*) the stratum zonale; *MFC*, the external division of the peduncle of the cerebellum (corpus restiforme); *SFC*, the internal division of the peduncle of the cerebellum; *Oi*, *Oe*, internal and external accessory olivary bodies; *R*, raphé; *MFJ*, internal divi-

But the circumstance that the corpus restiforme, or *external* division of the peduncle of the cerebellum, as it proceeds from above downwards (fig. 257, *MFC;* in fig. 258, the continuation of *Z* lying behind *S*) becomes exhausted, and vanishes, in proportion as the cross section of the cuneate and slender columns, *i.e.*, the posterior column, increases (fig. 258, *H*, that is, *Cn* + *Gr*), justifies and even necessitates the view that in these two sectional areas we have different portions of the course of *a continuous tract*, viz., a decussating *mode of origin* of the *posterior column* from the cerebellum. Preserving the idea of Deiters as a groundwork, the following view of this connection appears to me to be justified.

There are two courses pursued by these fasciculi of origin of the posterior column in the medulla oblongata.

1. The *external and middle* fibræ arcuatæ proceeding from the corpus restiforme are analogous to the *corpus trapezoides* of the superior olivary body. Having arisen from the cerebellum, they invest on the one hand the transverse section of the fifth (*S*) and the olivary body as the *stratum zonale;* and upon the other hand they perforate both the transverse section of the fifth and the olivary body, without, however, being connected with the nerve corpuscles of the latter. At the same time, as transverse fasciculi they include small nerve corpuscles within the transverse section of the fifth, and are continuous with the clusters of the motor area (nucleus of the lateral column).

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sion of the motor area (anterior column); *MFE*, external division of the motor area (lateral column); *G*, gelatinous substance; *S*, fasciculi in and around the gelatinous substance, which are the ascending roots of the fifth; *As*, fibræ arcuatæ that are continuous with the internal division of the peduncle of the cerebellum; *Am*, fibræ arcuatæ continuous with the outer division of the same peduncle; *XII*, roots of the hypoglossus; *X*, rootlets of the vagus traversing the gelatinous substance; the *X* beneath the grey floor indicates portions of the latter that emerge from the raphé in connection with the roots of the hypoglossal; X^1, fasciculi from the posterior columns of origin of the vagus; X^2, the anterior nucleus of the vagus, with fasciculi curving round in the rootlets of the vagus beneath the grey floor; X^4, fasciculi which, proceeding from the raphé beneath the epithelium of the grey floor, run round and through the eminentia teres; X^3, median nucleus; *VIII*, fasciculus belonging to the auditory nerve (Clarke).

These fibræ arcuatæ proceeding from the corpus restiforme cross the median line (partly running in front of, and partly out of, the hilus of the olivary body), and penetrate the opposite surface of the *other olivary body* in order to *join its nerve corpuscles*. The *crossed* connection of the *corpora restiformia* with the *olivary bodies* was admitted by Deiters, on the ground that both olivary bodies contain, in addition to such fibræ arcuatæ as can be shown to be connected with their cells in teased-out preparations, arched fasciculi that simply traverse them. The pathological fact, that *atrophy* of one half of the *cerebellum* always coincides with *atrophy of the opposite inferior olivary body*, supports the same view. The more posterior *fibræ arcuatæ* proceeding from the cells of the olivary body are continued into the cuneate and slender fasciculi (on the opposite side to their cerebellar origin), curving, after interlacement of their nuclei, around the transverse section of these columns. They augment the size of these columns by degrees to so great an extent that they approximate to one another behind the central grey substance of both sides, till they touch in the middle line on either side of the posterior fissure (fig. 258, *Gr*).

2. The *most posterior* of the fibræ arcuatæ which thus pass into the posterior column, it is obvious, cannot be connected with the olivary body on the same side, because the whole of this part of their course from the raphé to that column lies behind the olivary body. There are circumstances, however, that seem to show that these posterior fibræ arcuatæ have traversed the opposite olivary body on the other side of the raphé: for they do not pass transversely across the raphé, but, in their course from one side of the medulla oblongata into the opposite posterior columns, they pursue a long course, from before backwards, partly within the raphé as fibræ rectæ (fig. 258, *R*), partly, before their median decussation, within the transverse section of the anterior column, where they run in a radiating direction from before and outward towards the raphé; so that in their decussating course they really must have passed the region of the olivary bodies. This division of the fibræ arcuatæ in particular stands in connection with the large scattered cells of the motor area. Thus the *most poste-*

riorly situated fibræ arcuatæ, which pass out from the *corpus restiforme*, traverse the *olivary body* of their own side, and, running *behind* the *olivary body* on the other side of the raphé, enter, after junction with the *large scattered cells*, the *posterior column*.

Having entered the area of the posterior column, these collected fasciculi undergo fresh interruption with cell clusters which, enclosed by them in a plexiform manner, confer a peculiar grained or striated (geflammten) appearance upon this area, and divide beneath the floor of the fourth ventricle into two groups that coalesce anteriorly—the nucleus of the *cuneate column* and the nucleus of the *slender fasciculus* (fig. 258, *Cn*, *Gr*). The cells of these nuclei are for the most part of small size (24 μ in length, and from 6 to 9 μ in breadth), while only a very well-defined semi-circular mass of the outermost and most posterior groups of cells found in the cuneate fasciculus consists of large nerve corpuscles having a long diameter of from 30 to 36 μ, and a thickness of 15 μ.

The various directions pursued by the fibræ transversæ proceeding from the peduncle of the cerebellum, obviously associates them with the projection-fasciculi descending in the tract of the tegmentum. And it further appears that they are by no means merely in juxtaposition, and without action upon one another, since they are connected by the above-described *clusters of small cells*, by the *olivary bodies*, and perhaps also by the *scattered large cells*.

The relations that the interlacements above the superior olivary body and its region may have to the fasciculi of the spinal cord can scarcely be estimated, since the morphological characters are still perhaps only imperfectly known; or, granting that they are understood, these tracts also terminate in the cerebellum, which gives us no clue to the direction in which they act as conductors.

On the other hand, the *interlaced fasciculi* in the *medulla oblongata*, which pass into the posterior column, clearly constitute a *centripetal* tract, and their connection with the clusters (nuclei of the lateral column) lying on the other side of the raphé would subject certain myelonal fasciculi of the tegmentum to a here decussating reflex influence, just as this tract is probably accessible to such influence proceeding from the fifth nerve, both in its ganglia of origin and in the crus cerebri.

We are equally justified in believing that certain fasciculi of the projection-system which demonstrably pass from the crus cerebri into

the olivary bodies, are continued through the cells of the latter, or by tracts that still remain to be discovered, to the motor centres of origin of the cerebral nerves. Deiters indeed considered the longitudinal fasciculi of the crus cerebri connected with the olivary bodies to be a prolongation of the posterior columns into the cerebrum. This view, however, is by no means in accordance with the morphological appearances, inasmuch as (p. 469) the fasciculi of the tegmental tract penetrating the olivary body proceed from the centre of areas which, in the form of the layers of the fillet and motor area, pass into the antero-lateral tract of the spinal cord. Thus the idea of the local distinctness of the centrifugal and centripetal conducting tracts in the mosaic presented by the transverse section of these areas must be entirely dropped if the relation of the inferior olivary body to the projection system in the sense of Deiters be accepted; a conclusion which requires more convincing arguments for its acceptance than have hitherto been adduced in its favour. Reference will hereafter be made to the possible significance of the larger scattered cells.

ORIGIN OF THE CEREBRAL NERVES, FROM THE FIFTH TO THE TWELFTH.

The *system of the cerebral peduncle* (Hirnschenkelsystem) undergoes *diminution* within the territory of *interlacement of the cerebellar peduncles* (Durchflechtungs-gebietes der Kleinhirnarme) to the extent of those fascicular portions which, representing the musculature and the sensory surfaces of the head, reach their terminus in the grey matter of the central cavities of this portion of the brain. Their terminal masses at the same time serve (the fasciculi increasing in number) as the point of origin of the third link of the projection-system belonging to them, *i.e.*, the cerebral nerves, which has been already discussed in reference to the nucleus of the third and fourth nerves.

Just as the columnar portions of the cerebral peduncle which become the spinal cord, so also will the columnar portions which represent the cerebral nerves, present a duplicity of course in the anterior and posterior tracts of the cerebral peduncle, corresponding to their relations to consciousness on the one hand, and to their reflectorial relations on the other.

The areas in the mosaic of the transverse section, which belong to the cerebral nerves, are still indeed unknown; and

only so far as a crossed conduction can be definitively admitted for the tract of the crusta, and, as it can be shown that this decussation is effected by the straight fibres of the raphé, can we be certain that the columnar portions in question constitute the innermost fasciculi of the anterior longitudinal fasciculi of the pons and of the pyramids *before their entrance into the raphé*, and were perhaps the same ever since their descent in the cerebral peduncle (p. 419, fillet or loop of the cerebral peduncle).

But inasmuch as for reflex actions a crossed arrangement cannot be completely taken for granted, this argument is wanting to determine the localization of the columns of the cerebral nerves within the area of the posterior division of the pons and medulla oblongata, and the view of Schröder v. d. Kolk, that the actions in question are effected by the sectional area situated between the raphé and the hypoglossus, obtains no support from facts, except in the undeniable diminution of this area downwards. We know, however, the *place* better than the *mode* of the termination of these portions of the crus cerebri, the former being indicated by the origins of the cerebral nerves from the same spots.

A great part of these so-called nerve nuclei, the relations of which to the roots Stilling did good service in discovering, belong to the grey floor of the fourth ventricle, which, in consequence of their projections and intervening furrows, acquires a well-marked division into areas. This rhomboidal space (fourth ventricle) formed by the convergence of the superior peduncles above, and the fasciculi graciles below, is divided by *the median furrow*, (*the calamus scriptorius*,) into two symmetrical lateral halves, and by the *striæ medullares* (or if these fail, by an imaginary line connecting the two auditory nerves) into an upper and a lower half.

The superior angle of the fourth ventricle, as it gradually expands, exhibits, in addition to the eminentiæ teretes belonging to the aquæductus, a furrow extending laterally as a sharp angle between the floor and the lateral wall, through the ependyma of which the dark cells of the substantia ferruginea (figs. 250 and 252, *F*, 5) glimmer of a bluish colour, in accordance with the laws of refraction of light through cloudy media. This is the *fossa cærulea*. As the pigmented cell clusters belong to the

fifth nerve, we have here again a manifestation of the lateral position of the sensory columns of origin. At a height of about six millimeters above the striæ medullares, in the region where the internal surface of the superior peduncle is covered by fasciculi of the internal division of the peduncle of the cerebellum (fig. 255, *H'*), a furrow commences which presents an obtuse angle internally, and forms externally a rhombic space on the grey floor (fig. 254, where its transverse section is shown at 8). This is the *internal auditory nucleus* of Clarke, the upper and larger triangular half of which Stilling also recognized as such, whilst the half belonging to the lower angle of the floor of the fourth ventricle he regarded as the *nucleus* of the *glossopharyngeus*. The broad median portion of this groove is situated in the region of the medullary striæ of the *auditory nerve*. Internally to the nucleus of the auditory nerve, the motor column of the grey matter exhibits above the region of the striæ an oval eminence, which Stilling and Clarke agree in considering the common nucleus of the *facial and sixth pair* (fig. 254, at *G*).

The furrow dividing the upper half of the rhombic nucleus of the auditory nerve and the last-named oval eminence is not seldom rendered still more apparent by the presence of the *ascending medullary striæ* of J. Engel, which run parallel to the furrow upwards and outwards from the internal extremity of the striæ acusticæ. These are the *crossed prolongation* of the auditory roots into the opposite cerebellar peduncle, or more correctly speaking, they are the *superficial crossed fasciculi of origin* of the *auditory nerve* from the *cerebellum*. In many instances only the innermost fasciculus of the *ascending medullary striæ* just external to the common nucleus of the facial and abducens nerves is visible, for which the name selected by Bergmann, of "sound rod" (Klangstab), should be restored, since Stilling's explanation of its being an inconstant posterior root of the fifth must be given up. The uniform absence of the medullary striæ in animals does not indicate that their fasciculi do not exist, but only that they are not visible, as they may remain as naked axis-cylinders without medullary sheaths. The development of these medullary sheaths occurs when the evolution of the brain is complete, and therefore they

fail in the newly born, and are most commonly found, according to J. Engel, in the bodies of those who have arrived at the adult period of life. For the same reason the crusta of the cerebral peduncle in the newly born presents a grey instead of a white colour. The circumstance of the white medullary substance developing at different periods in the several parts of the child's brain suggests itself as a subject of sufficient importance to demand a searching investigation.

The nucleus common to the vagus and accessory nerves of Stilling and Clarke appears at the lower angle of the fourth ventricle between the median elevation, chiefly produced by the *nucleus* of the motor *hypoglossal nerve,* and the *internal auditory nucleus* of Clarke, and constitutes, according to Deiters, the nucleus of origin of a *median and lateral system* of mixed nerve roots. In consequence of its dipping at the upper extremity of the calamus scriptorius between the auditory nucleus and Stilling's nucleus of the hypoglossal nerve (seen in fig. 257, X^1, between the lateral and median eminence), it gradually vanishes so as to form, when seen from the fourth ventricle, a triangle with the apex above; and in the same manner the region of the hypoglossal nucleus forms a triangle with the apex downwards, because as it descends it becomes progressively more and more covered by the nucleus common to the vagus and accessory nerves, which comes down to the middle line behind it. (Compare fig. 257 with fig. 258.)

These morphological relations coincide with the gradual deepening of the fourth ventricle, so as to form a closed central canal. The nucleus of the vagus becomes exposed, and appears in the form of a mass of grey matter, Arnold's ala cinerea, covered only by the ependyma. The *nucleus* of the *hypoglossus,* however, is not thus exposed, but is invested by medullary fasciculi (fig. 257, X^4), the white substance of which is sharply differentiated from the grey of the ala cinerea, and which belong to the origin of the vagus and accessory nerves. Their centre of origin at the same time (the eminentia teres of Clarke) is superjacent to the hypoglossal nucleus, so that the elevation named medial by Stilling cannot be considered as the hypoglossal nucleus itself, but only as the region

in its *vicinity*. The nuclei common to the vagus and accessory nerves are connected below in the form of a horse-shoe curving round the bolt commissure (Riegels-Obex) (Clarke, Deiters) (fig. 258, *Ob*), the fasciculi of which cause the external border of the lower half of this nucleus to project, and appear in the fourth ventricle, though more constantly in Mammals than in Man.*

The obex is concentrically surrounded by the adhering border of the embryonic roof of the fourth ventricle, the tæniola (Riemchen),—which proceeds from the substance of the slender column. The roof of the fourth ventricle continuous with it, investing the auditory nerve, cuts off two lateral diverticula of the fourth ventricle, which, according to Reichert, are the analogues of the lateral ventricles.

The fourth ventricle of Mammals (excluding Monkeys), on account of the absence of the striæ and the slighter projection inwards of the auditory nucleus, renders the region of origin of the facial and hypoglossal nerves far more evidently a continuation of the median motor column (Lenhossek) than in Man. Moreover their shallow slightly excavated fourth ventricle wants the apex of the calamus scriptorius, since the lower extremity of the hypoglossal nucleus, in consequence of the insignificant alæ cinereæ, remains broader, and has a curved boundary in the transverse projection of the obex.

The posterior division of the pons contains below its greatest convexity, (at those planes, namely, which are defined posteriorly by the superior peduncle no longer covered by the loop, and which lie anteriorly below the emergence of the fifth between the transverse fasciculi of the middle peduncle), one after the other, the origin of the fifth, sixth, and seventh, and lastly of the eighth pair of cerebral nerves.

The *small root of the fifth* arises from the uppermost of these origins, the superior trigeminal nucleus of Stilling, which forms, in the lateral regions of the motor area in front of the descending roots of the sensory portion of the fifth, internally to its point of emergence, and behind the fillet, an oblong

* For a fuller account and representation of the obex (Clarke's *slender column* connected with the vagus and spinal accessory), see Clarke's *Researches on the Brain*, in *Phil. Trans.*, 1868, Part i., pp. 274, 275, and 276. Plate x., figs. 25, 27, 30.

area in transverse section, composed of large (60 to 75 μ long and 18 to 21 μ broad), delicate, multicaudate nerve corpuscles (figs. 252 on the right side, and 253 on the left, 5 *m*). This nucleus is three millimeters in vertical height, has a transverse diameter of 1·5 millimeters, and an anterior-posterior diameter of rather more than 1·5 millimeters. Its inferior rounded portion, having a diameter of only 0·8 of a millimeter, forms an appendix, separated only by a short interval.

The only obvious connection this nucleus possesses is with the fasciculi of the internal roots of the fifth, which, in consequence of their being, at their emergence from the pons, directed obliquely forwards and upwards, appear in transverse section as short obliquely longitudinal fasciculi, between which the long processes of the nerve corpuscles can often be followed for a considerable distance.

In general terms, the connection of this nucleus with the crusta is effected by the numerous fibræ rectæ of the raphé occurring at the planes of origin, and which pass from the anterior division of the pons into the posterior, as well as by its connection with isolated elongated cells, equal in size to those of the nucleus, all which conditions will repeat themselves in the case of the hypoglossal nerve, and may be regarded as a scattering of its cells of origin in the raphé. In order, however, to attain the motor nucleus of the fifth nerve, the fibræ rectæ must here reach their termini as a posterior portion of those fibræ arcuatæ that belong to the planes of the fifth. In favour of this supposition is the inclination forwards of the inner ends of many fibræ arcuatæ.

Our knowledge is equally limited in regard to the tracts through which reflex influences act on the upper nucleus of the fifth. Clarke was the first to point out the similar relations presented by the sensory root of the fifth, and it is easy to conceive that we have here a repetition of the type of the spinal cord, because the large nucleus of origin of the fifth (fig. 253, *g*, on the left side) corresponds to the caput of the posterior cornu, and the superior nucleus of the fifth to the anterior cornu (to its processus lateralis). Clarke, however, has not been actually able to discover such connections, because his account does not, on the one hand, embrace the region of the true motor root of

the fifth; and, on the other, the nucleus he observed to be connected with the gelatinous substance is not the nucleus of the fifth, but the inferior nucleus of the facial nerve. He does not allude to any connection as existing with the lowermost point

Fig. 253.

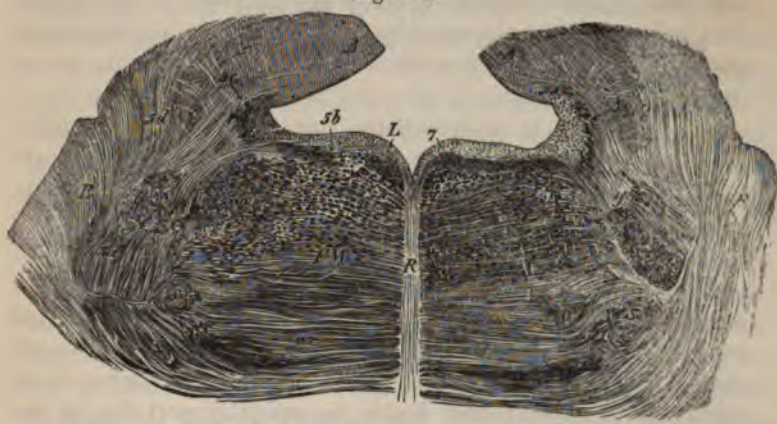

Fig. 253. Transparent transverse section from the pons of Man, at the planes of origin of the great root of the fifth: the right half of the figure represents a somewhat lower plane than the left. *A*, Superior peduncle of the cerebellum (Bindearm); *L*, the posterior longitudinal fasciculi beneath the grey floor of the fourth ventricle, the left overlaid with fasciculi of the fifth nerve proceeding from the raphé; 7, fasciculi of the root of the facial posterior to the posterior longitudinal fasciculi, and continuous internally with the fibræ rectæ of the raphé, and running in close connection with descending fasciculi of the fifth; *B*, the middle peduncle of the cerebellum (Brückenarm); *F M*, the motor area of the posterior division of the pons; *ar*, fibræ arcuatæ; *R*, the raphé; *S*, the region in which the inferior lamina of the fillet bends round; *g*, the gelatinous substance of the origin of the fifth; 5 *a*, the great root of the fifth; 5 *b*, the internal descending roots of the fifth; 5 *c*, external descending roots of the fifth; 5 *d*, roots of the fifth proceeding from the cerebellum; 5 *m*, nucleus of origin of the small root of the fifth; *Q*, transverse section of the ascending roots of the fifth that lie just external to the fasc culi of the latter at their point of emergence; *O*, region of the superior olivary body.

of the true motor root of the fifth, which I recognize in section as a small cluster of cells situated not unfrequently at a considerable distance behind the inferior nucleus of the facial. On

the other hand, such reflex influences may undoubtedly occur through root-fasciculi proceeding from some other of the manifold masses of origin of the fifth pair. To institute a comparison between the whole series of these masses, and the relations presented by the origins of the posterior roots of the spinal cord, and to refer it to the type of the cord, is an important and still unaccomplished work that awaits monographic investigation.

The reflectorial relations of the motor nucleus of the fifth, as we may conclude from the phenomenon of trismus, must embrace the sensory region of the spinal cord, and it is on this account probable that certain portions of the fibræ arcuatæ of these planes, notwithstanding that we are unable to trace them into transverse sections of downward tending masses, may still turn out to be tracts of origin of the posterior columns. Possibly we must regard the large scattered nerve corpuscles in the motor area, which are here somewhat more numerous than at higher levels, as outlying portions of the superior nucleus of the fifth, which connect it with the fasciculi of the posterior column, here appearing as fibræ arcuatæ.

The multiple origin of the *external large sensory root of the fifth* will best be understood by recognizing four separate and principal forms of origin.

1. *Roots of the fifth, the nuclei of origin of which are situated within, or not far distant from, the plane of emergence.* The nucleus of origin of this very remarkable tract embraces in longitudinal section the outer side of the motor root of the fifth in a semilunar manner. In Man it possesses a vertical length of 4·4 millimeters, with a transverse diameter of 1·2 millimeters, and an antero-posterior diameter of 2·8 millimeters.

It is composed of small clusters that are separated from one another by the delicate fasciculi of origin of the nerve which arise in a plexiform manner from the nerve corpuscles (fig. 253 *g*, 5 *a*). The matrix in which these clusters lie consists of finely granular connective tissue, and the nerve corpuscles for the most part have a length of 18 to 24 μ, and a thickness of 6 to 9 μ. Stilling correctly regards the whole formation as a continuation of the gelatinous substance which extends down continuously as far as the caput of the posterior cornu

of the spinal cord, enveloped by the ascending root of the fifth nerve.

The innermost clusters of these masses that are approximated to the motor root of the fifth, present cell elements of a larger calibre, having a length of 39 μ, and a thickness of 12 μ; so that from the motor nucleus of the fifth, as far as to the external clusters of the just-described masses, we have a repetition of the three different-sized nerve corpuscles that are contained respectively in the anterior cornu, in the root, and in the caput of the posterior cornu of the spinal cord.

2. *Roots of the fifth, the nuclei of origin of which are situated above the plane of emergence. Descending Roots.* The descending roots of the fifth are divisible into three portions.

The external descending root of the fifth (figs. 249, *V*; 250, 251, 5; 252 and 253, 5 *c*) arises from the region of the nates, as far down as to the point of emergence of the fifth, out of those large vesicular cells, from which, on the other hand, the already described (p. 452) interlacement of the tegmentum proceeds. It descends outside the central grey matter around the aquæduct, and, continuously augmenting in size, is enclosed, while in the pons, in that lateral region of the grey floor which creeps along the internal surface of the superior peduncle. Upon the inner border of its semilunar area, which Stilling and Deiters considered to be an ascending root of the fourth, grape-like clusters of corpuscles are situated, forming a continuous chain, the elements of which are distinguished from those of the substantia ferruginea by their spheroidal form and the absence of pigment (p. 447).

The middle portion of the descending roots of the fifth proceeds from the cells of the substantia ferruginea. This elongated cluster of pigmented fusiform (60 μ long, 20—30 μ thick) nerve corpuscles, which in the Locus cæruleus glimmers through the grey floor, commences in the lower half of the testes, and extends downwards for more than a centimeter to just above the emergence of the motor roots of the fifth, being always situated internally to the *outer* descending roots (figs. 250, 251, 252, *F*). Scattered fragments of this compact formation, however, extend into the lateral regions of the posterior division

of the pons in the form of large richly pigmented bodies arranged radially to the grey floor, with radial nerve fibres running to meet it; perhaps in their course (which will presently be described) they also contribute roots to the fifth. Black pigmented cells are found similarly scattered in the roof of the fourth ventricle internally to the superior peduncle (substantia ferruginea superior). In the brains of children, and in those of Mammals, these cells lose their pigment, like those of Soemmering's substance, and indeed in many corpuscles of this formation pigment does not appear to be developed.

The fasciculi of the fifth, proceeding from the substantia ferruginea, form a stratum having a thickness of 0·8 of a millimeter which runs transversely inward beneath the grey floor of the fourth ventricle; they then penetrate, interlace with, and encircle, the posterior longitudinal fasciculi, and finally cross the median line by means of an acute-angled decussation passing partly between and partly in front of the posterior longitudinal fasciculi, the decussating fibres being at the same time arched, with their convexity directed upwards. Having arrived at the opposite side, they pass outward, partly through and partly in front of the other posterior longitudinal fasciculi, and turn forward to enter the tract of the great root of the fifth as the middle set of the chain of fasciculi surrounding the grey floor (figs. 252, 253, 5 *b*).

Both the interlacement of the posterior longitudinal fasciculus seen on transverse section, and, in particular, the region surrounding it anteriorly, as far as to the margin of the posterior division of the pons, is very rich in nerve corpuscles of a large size, that are sparingly present, and of a far smaller variety that are more closely clustered. The *middle* descending root of the fifth appears to me to be continuous with the larger form of corpuscles.

The internal division of the descending roots of the fifth is derived, in all probability, from the longitudinal fasciculi of the anterior division of the pons (crusta of the cerebral peduncle), and runs in the form of straight fasciculi of the raphé from the anterior division of the pons into the posterior. After undergoing decussation at acute angles, the fasciculi curve partly in front of the posterior longitudinal fasciculi, partly run trans-

versely through, and partly behind them, and attach themselves to the fifth to form the innermost of those of its roots, which are covered by the grey floor of the fourth ventricle, being situated between the posterior longitudinal fasciculi and the middle descending roots (figs. 252, on the right side, *L;* 253, on the left side, *RL*). The transverse decussating fasciculi of the middle, and the straight fasciculi of the internal, descending roots, do not appear to mingle in the raphé, but the former, bending to make way for the latter, pass above them. The internal descending roots are continuous with the formations of smaller nerve corpuscles situated in front of and behind the longitudinal fasciculi.

Stilling derived the two last-mentioned portions of the origin of the fifth simply from the grey substance of the floor. I myself formerly attributed their origin to radiating fibres from the medulla of the hemispheres, which associate themselves externally, above the planes of section represented in fig. 248, below the optic thalami, with the posterior longitudinal fasciculus, and descend with it. Inasmuch as these fasciculi extend downwards between the external descending root of the fifth and the posterior longitudinal fasciculus, from which region so important an addition passes to the great root of the fifth, I formerly regarded them as portions of this root. But after I had acquired a knowledge of the mode in which the medullary fibres proceeding from the substantia ferruginea reach beneath the grey floor of the opposite side, I comprehended that those lateral posterior fasciculi of the tegmentum, externally to the posterior longitudinal fasciculi, were indeed covered and interlaced by the actually descending roots of the fifth, but could not constitute the roots of the fifth.

3. *A root of the fifth, the nucleus of origin of which is situated below the plane of emergence (ascending root of the fifth).* Corresponding to the point of emergence of the fifth (fig. 253, *G Q*), external to the tegmentum and internal to the fibres from the cerebellum, as far as to the lowest segments of the medulla oblongata, is a compressed mass of transversely divided fibres, the extremities of which must obviously lie in the origin of the fifth (figs. 254, 255, 256, 257, 258, *S G*). The sectional area of these fibres includes in its concavity, which is turned backwards, grey matter containing for the most part small nerve corpuscles, in which, after breaking up into delicate fasciculi,

the fibres become lost at the lower extremity of the medulla oblongata, and around which at the same point the lateral and the posterior columns of the spinal cord coalesce. It is consequently recognizable as the gelatinous substance or caput cornu. The quantity of this gelatinous substance appears to have undergone extraordinary increase in the lower half of the medulla oblongata, being accumulated to form the grey tubercle of Rolando, because at these levels the chief portion of the ascending root of the fifth is developed from it as a centre (figs. 261, 262, *G*). Nerve corpuscles of larger calibre, foreign to the gelatinous formation, but which are included in it at various heights of the pons and medulla oblongata, I am of opinion, may be regarded as introduced by traversing masses of the fibræ arcuatæ, and in part by traversing nerve roots.

4. *Cerebellar roots of the fifth.*—These fasciculi, that in all probability enter the fifth pair of nerves, traverse and embrace the superior peduncle of the cerebellum, and Stilling has already ascribed a similar course to them (figs. 252, 253, 5 *d*).

It is certainly satisfactory to find that in the mode of origin of a pair of nerves connected with so many and various peripheral regions a corresponding multiplicity of anatomical relations can be established. On the other hand, however, while giving the objective enumeration of these origins, such considerations must be neglected, because for the present we possess no sufficient grounds for a systematic theory furnishing a key to their comprehension.

Below the origin of the fifth, the grey floor of the fourth ventricle is divided by symmetrical lateral grooves into the median territory of origin of the sixth and seventh cerebral nerves, and into the lateral origin of the auditory nerve (fig. 254, *G* and 8).

The *nervus abducens* (fig. 254, 6) springs from Stilling's *abducens-facialis nucleus*, a cluster of slender multicaudate nerve corpuscles (fig. 254, on the left side, in front of *G*) two millimeters broad and 1·6 millimeters thick in section, the cells of which have for the most part a length of 45 μ, and a breadth of 15 μ.

This nucleus, according to Stilling and Schröder v. d. Kolk, is connected with the raphé by means of the most posterior fibræ arcuatæ. By following up the fasciculi I have satisfied

myself that even those fibræ rectæ of the raphé, which, proceeding from the region of the abducens-facialis nucleus, run obliquely downwards towards the medulla oblongata, curve round at the lower border of the pons, and run with the pyramids into the crus cerebri.

The abducens-facialis will consequently be subject to the crossed influence of the centres of origin of the crusta of the crus cerebri.

The roots of the sixth proceed from this nucleus in the form of fine separate fibres from a portion of the pons, of 1·4 millimeters in height, and, running in an antero-posterior direction parallel and close to the raphé, reach the posterior division of the pons, and pass from thence obliquely downwards to their well-known position in the basis cerebri. The external fasciculi of the central root of the abducens, that lie in the anterior part of the nucleus, obviously proceed from its nerve corpuscles, and form arches directed internally. The internal fasciculi, however, appear to embrace the nucleus as a compact medullary layer in which only a few nerve corpuscles are distributed. I believe I have satisfactorily convinced myself that these fasciculi also simply proceed from the same nucleus, although they describe almost a complete circle around their origin.

The nucleus of the sixth, with the fasciculi of its root, would consequently represent a glomerulus or knot analogous to the nucleus of the hypoglossus (fig. 258, XII).

The central extremity of this knot, like the latter, would be found in those fibræ rectæ of the raphé which enter the nucleus of the sixth as posterior fibræ arcuatæ. These fasciculi of the crus cerebri encircle the nuclear mass on its anterior and external surfaces, are interrupted by the nerve corpuscles, and following the convolution of the knot pursue their course to the root fasciculi by means of which the circle which they form around the nucleus is completed in its posterior and internal parts. The difficulty that is experienced in bringing into view the continuity of this course in sections is due especially to the circumstance that the course pursued by each fibre of this knot in the raphé belongs to lower planes of section than the root extremities of these fibres; and hence in the right half

of fig. 254, which represents a higher level than the left, roots of the sixth are already visible without any part of its nucleus being apparent.

Whether additional root fasciculi of the sixth proceed, as Schröder v. d. Kolk maintains, from some unknown centre of origin situated above and external to this nucleus must remain at present undecided. The same writer made the plausible remark that the course of the root of the sixth, directed as it is *from* the raphé, indicated (in opposition to the apparent tendency of the oculomotorius to effect a decussation in the raphé) a non-decussating central origin of the sixth, by which means its synergetic action with the opposite rectus internus would be explained. If, however, the origin of the sixth is as I have stated, this observation is no longer applicable to it, however correct the principle may be in reference to anatomically preformed co-ordinations of movement, as indeed I have recognized in the partly decussating, partly non-decussating origin of the tegmentum of the crus cerebri. That this principle, however, is not applicable to the innervation through the crusta of the crus cerebri, I have already stated in general terms on p. 453 *et seq.*, and no exceptional conditions would obtain in the case of the nucleus of the sixth, merely on account of its connection with the raphé.

But whether the abducens receives its nerves decussatingly or directly from determinate centres of co-ordination (corpora quadrigemina) may be decided by the investigation of the relations of descending tracts to it even at a totally different level. The interesting fact discovered by Gudden is perhaps of importance in regard to the control exercised over the abducens by a centre far removed from it at the level of the origin of the oculomotorius, that a flat fasciculus proceeding from the nates enters transversely into the crus cerebri (tractus transversus pedunculi), which only became very feebly developed when Gudden destroyed the function of the retina in newly born animals, and certainly therefore stands in close functional relation with it. The fasciculus itself had already been observed and correctly delineated by Inzani and Lemoigne.

Clarke also considers that root-fasciculi of the nervus abducens curve round the transverse section of the nucleus of the facial, and

that they arise in a fine brush-like expansion from the eminentia teres.

The roots of the *facial nerve* have a multiple origin, which will be most readily understood from the following division :—

Fig. 254.

Fig. 254. Transparent transverse section from the pons of Man, at the planes of origin of the facial and abducent nerves ; the right half represents a somewhat higher plane of section than the left. *Cbl*, Cerebellar mass forming the roof of the fourth ventricle ; *Zc*, the projection of the internal division of the peduncle of the cerebellum as it passes from the cerebellum ; *Cr*, the projection of the corpus restiforme from the cerebellum ; *R*, the raphé of the posterior division of the pons ; *VS*, the transverse section of the motor portion of the same ; *S*, the transverse section of the sensory portion of the same, containing the ascending roots of the fifth ; *O*, the superior olivary body ; *Br*, the brachium of the pons ; *Trp*, its deep, *Trs*, its superficial layers of transverse fasciculi ; *P*, the anterior longitudinal fasciculi of the pons ; 7, the roots of the facial nerve ; *G*, the genu of the facial nerve ; 7^1, the posterior (superior) nucleus of the facial, or nucleus common to the facial and abducens ; 7^2, the anterior (inferior) nucleus of the facial ; 6, root of the abducens ; 8, region of the internal auditory nucleus in the transverse section of the grey floor of the fourth ventricle.

1. *Roots of the facial, the nucleus of origin of which is situated above their plane of emergence. Descending roots.*—

These fibres, arising from the raphé, decussate and run forwards as its fibræ rectæ, forming arches with their convexity upwards, and pass (curving over the facialis abducens nucleus) uninterruptedly into the roots of the facial nerve (fig. 254, on the right side, where they appear as light fasciculi in front of the dark area *G*). In consequence of this curve their continuity with the root is only visible in the uppermost planes of section of the region of origin of the nerve; in those made at a lower level the crown of the arch is removed. A few of these descending root fasciculi do not run within the raphé, but through the motor area, and, decussating with the fibræ arcuatæ, become associated with the other roots of the facial (fig. 254, on the right side, between *R* and 6). It naturally remains uncertain whether the fasciculi have a common origin—say, in the lenticular nucleus—with those roots of the facial which run as fibræ rectæ of the raphé.

2. *Roots of the facial, the nucleus of origin of which is situated at the level of the plane of emergence.*—These fasciculi, though not admitted by Deiters, arise from the nucleus common to the abducens and facialis, and indeed from its upper half alone, so that it is not unlikely that the connection of the facialis with this nucleus may be called in question when sections are made through a somewhat lower plane. As far down, however, as this connection can be traced, the root fasciculi of the facial emerge from the nucleus in a very characteristic manner, their expansion corresponding exactly with the height of the nucleus itself (fig. 254, on the left).

3. *Roots of the facial, the nucleus of origin of which is situated below the plane of emergence. Ascending roots.*—Dean and Deiters have given independent descriptions of the course of these fibres, and sufficiently correct, so far at least as can be ascertained from the unfinished work of the latter. Clarke has also thoroughly investigated their relations, and errs only in regarding the superior olivary body as their nucleus of origin, instead of the inferior facial nucleus, which he has mistaken for the motor nucleus of the fifth. Their nucleus origin is the anterior (inferior) nucleus of the facial, a cluster of slender multicaudate nerve corpuscles (of about 60 μ long and 21 μ broad), which, extending into the region of the abducens-facialis nucleus, has a length of 3·5 millimeters, and

reaches nearly as far as the lower border of the pons, measuring in a transverse direction 1·6 millimeters, and in the antero-posterior diameter 2·4 millimeters.

This nucleus lies just on the outer side of the superior olivary body, and appears sharply defined in Man (fig. 254, on the left side, 7), through the curvatures of a nuclear tract or convolution (Knauel) in which the fasciculi of origin are imbedded, *the central extremities* of which may connect the nucleus through the raphé with the *crus cerebri*. The nucleus, as a whole, is less sharply defined in animals, because the convolutions of which it is composed, are, like those in the glomeruli olfactorii, separated from each other by connective tissue (fig. 255, 7). The peripherically running fibres of the glomerulus run separately, and in small groups, forming a curve directed outwards as far as to the grey floor, and there collect into a geniculate compact fasciculus, with its convexity looking upwards—the facial genu of Deiters—which during its course of 5 millimeters occurs in all transverse sections to the inner side of and behind the root of the abducens, its nucleus appearing as a dark sharply defined area (fig. 254, on the left side, *G*). The genu, therefore, appears to be separated from the emerging root of the facial by these two structures, because it is continuous with the latter, by means of an arch (that curves over the facialis-abducens nucleus), and is consequently cut off at the crown. The ascending root of the facial repeats at its exit, about 5 millimeters higher up, the externally convex curve described by its fasciculi on leaving their nucleus (fig. 254, *G* 7, on the right side). Since the emerging roots of the facial spread themselves through a portion of the pons, measuring about 2 millimeters in height, their inferior fasciculi, it is obvious, must, in a series of transverse sections, be situated opposite to the geniculate portion (fig. 254, on the left side).

The ascending roots of the facial consequently form a fasciculus unconnected with the abducens nucleus, but which diverges to make way for this nucleus and the root of the abducens, and curves round them in the form of a *horseshoe*. The crura of this horseshoe lie in the pons superjacent and parallel to one another; the *inferior crus* conducts inwards and backwards to the genu the fasciculi procceding from the

anterior nucleus of the facial (fig. 255); the *superior* conducts them from the genu outwards and forwards to the point of emergence (fig. 254, on the right side). The genu forms a connecting piece at right angles to the two crura. The horse-shoe, however, in order to curve round the common nucleus (as far as its median surface), bends inwards at the intermediate piece (as if along the surface), and at the same time, in order to curve round the upper circumference of this nucleus, bends upwards to the upper crus (as though along the edge).

The uppermost arched fibres of the root of the facial, proceeding from the genu, extend upwards as far as to the origin of the fifth (fig. 253, 7); and hence the statement made by Stilling, that the genu of the facial was a constant posterior root of the fifth, and that its terminus was *an inferior trigeminal* instead of *a facial nucleus.*

The roots of the *auditory nerve* are met with at about the same plane as the origin of the ascending root of the facial (fig. 255, 8), and the following four formations of grey matter stand in connection with them in the pons:—

1. *The internal auditory nucleus* (Stilling, Clarke).—In this an upper, middle, and inferior plane are to be distinguished. The *upper* is situated externally to the arch of the superior nucleus of the facial (fig. 254, 8); the *middle* (corresponding nearly to the zone of the striæ medullares) includes the entire breadth of the rhomboidal space (fig. 255, VIII); and the *inferior* lies externally to the origin of the glossopharyngeus and to the nucleus of the vagus and accessory nerves (fig. 257, 8).

This nucleus is, of all the masses of the grey floor, the most closely interwoven with fine fasciculi, which for the most part extend from the cerebellar peduncle towards the raphé, and inclose the nerve corpuscles, which have a length of from 30 to 45 μ, and a breadth of from 12 to 15 μ.

2. *The external auditory nucleus* (Clarke, Dean) embraces the trapezoid area of the internal division of the crus cerebelli, which, applied immediately to the internal auditory nucleus (fig. 255, *H*, on the left side, behind 8^4 on the right side, fig. 257, *SFC*), has the anterior and posterior line of demarcation in common with it, and is in contact externally with the restiform body of the crus cerebri. The transverse section of the

Fig. 255.

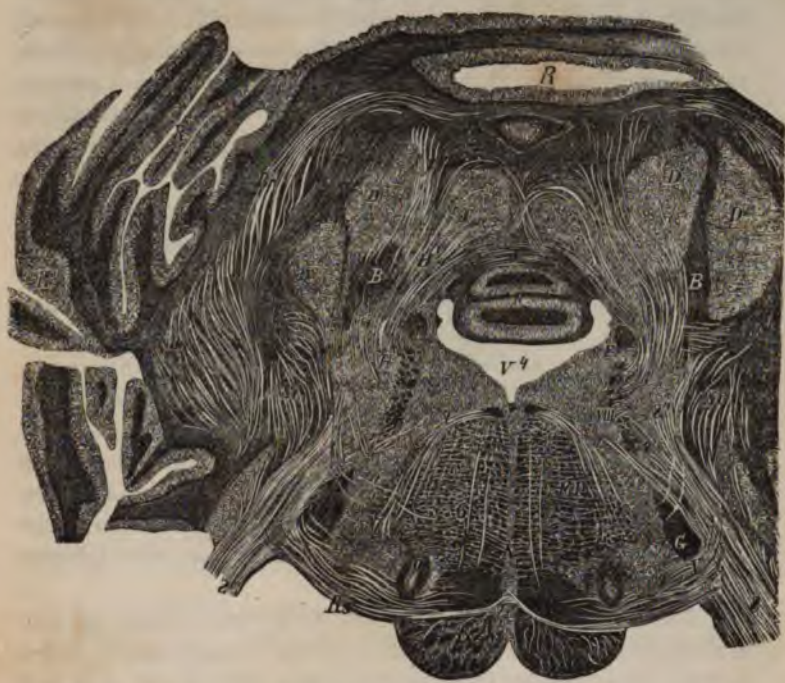

Fig. 255. Transparent transverse section of the cerebellum, and of the uppermost planes of the medulla oblongata of Cercocebus cinomolgus. Origin of the auditory nerve. The right half of the drawing represents a somewhat lower plane of section than the left. V^4, The fourth ventricle; *R R R*, the cortex of the left hemisphere, of the superior vermiform process and of the inferior vermiform process of the cerebellum; VIII, the internal nucleus of the auditory nerve; *N*, the raphé; *P*, the pyramid; *M F*, motor area of the posterior division of the medulla oblongata seen in section; *G V*, the gelatinous substance, with the ascending fasciculi of the root of the fifth; *a*, fibræ arcuatæ continuous with the internal division of the peduncle of the cerebellum; *H*, the fasciculi of the internal division of the peduncle of the cerebellum; *St*, the external division of the cerebellar peduncle (large cells appearing between the two divisions); *Br*, the arm of the pons (middle peduncle); *Rs*, corpus rhomboideum; *O*, sup. olivary body; 7′, inf. nucleus of the facial, on the outer side of the olive, from which the roots of the facial (7) proceed, and extend as far as beneath the grey floor into the area of the genu of the facial; 6, nervus abducens; 8, auditory nerve arising in 8^1 from the internal auditory nucleus on the grey floor, in

internal auditory nucleus is consequently only a smaller similar triangle, incompletely separated by the fasciculi of the internal division of the crus cerebelli from the general triangle which the confluent area of transverse section of the *external* nucleus forms with it. In its internal half this external nucleus is traversed by the internal division of the cerebellar peduncle, the areas of which are seen in transverse section; but the outer part is of a pure grey (fig. 255), and includes very numerous multicaudate slender nerve corpuscles, having a length of from 60—100 μ, and a thickness of 15—21 μ.

3. The *anterior auditory nucleus* (fig. 255, 8^2) is a wedge-shaped mass intercalated between the auditory nerve, the corpus restiforme, and the medulla of the flocculus, forming a triangular area three millimeters in height and two millimeters broad. It includes a large number of closely arranged vesicular nerve corpuscles with but few processes, that vary from 15—21 μ in size, and which, whilst differing from those of the interspinal ganglia in their small size, resemble them in their form and in their being enclosed in a sheath beset with delicate small nuclei.

4. *The nerve corpuscles of the auditory root.*—These are distributed either singly or in small clusters throughout its entire central course, but by their accumulation swell it out into the form of a ganglion at the point of its emergence at the anterior border of the pons, and are deposited to an equal extent in the external portion of the root which embraces the crus cerebelli. Their for the most part large size, their elongated and multicaudate form, and the absence of a capsule in them, prevent us from agreeing with Stilling and Clarke in considering that

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8^2 from Stilling's anterior auditory nucleus, in 8^3 from the internal division of the cerebellar peduncle, and in 8^4 from the external division of the same; *D*, the dentated nucleus in the cerebellum; *T*, the nucleus of the roof (Stilling) in the cerebellum; *B*, the medullary mass of the superior peduncle (processus e cerebello ad testes) in the cerebellum; H^1, fasciculi of the internal division of the cerebellar peduncle undergoing, and H^2 similar fasciculi apparently not undergoing, decussation; *F*, the peduncle of the flocculus on the right side, likewise as transverse sectional area and as oblique longitudinal fasciculi above the corpus restiforme.

they constitute a part of the same formation as the anterior nucleus.

In regard to the medullary masses connected with these nuclei it now becomes requisite to determine which of these last are to be regarded as centres of origin, and which as terminal masses, since they descend to them from masses that are still to be regarded as central.

In the first place, the auditory nerve offers no parallel on morphological grounds to the nearly allied and important sensorial regions of the olfactory lobes and the optic nerve. For no connecting arches pass from the pons for the formation of the labyrinth, or rather the organ of Corti, which can be considered as the morphological homologues of those which pass from the cortex of the cerebrum to the olfactory lobes and the retina.

While the medulla of the olfactory lobe and that of the retina (as the optic nerve) run with converging fibres presenting characters precisely similar to those of the upper link of the projection system into the same terminal ganglion as the white fibres coming from the cortex of the cerebrum, the auditory nerve does not extend to any of these ganglia, but enters into the grey matter of the central cavities, which is not immediately connected with the central lobes. Its immediate entrance into this structure, as well as its form, makes the auditory nerve analogous to the *nerve roots*, or to the inferior link of the projection system. It is not however justifiable on this account to associate the auditory nerve completely in the further details of its course with the other nerve roots of the peduncle of the cerebrum, and indirectly with the type of the spinal cord. Deiters attempted to do this when he explained both as members belonging to its lateral mixed system, the other formations of which are represented by the glossopharyngeal pneumogastric and accessory nerves, which are in the same manner neither purely sensory nor purely motor. In adopting this view, he only rehabilitated the old statements of Galen, Fallopius, and Haller, according to whom the auditory nerve, as the portio mollis formed a common nerve root with the facial nerve.

Deiters assigned this position to the auditory nerve in

the idea that the origin of the auditory nerve from the cerebellum, already expressed in general terms by Foville and Schröder v. der Kolk, might be rejected. I must however insist, before entering into details, that the exclusive partly decussating, partly non-decussating connection of the auditory nerve with the cerebellum indicates that it belongs *to a different category from the other nerve roots;* in favour of which view, which I have long maintained, and have supported on microscopic grounds, I may adduce the experience of Clarke and Dean.

In accordance with the general plan of this essay, I ought in the next place to refer to the tracts that connect the cerebral lobes through the peduncle with the centres of origin of the auditory nerve, a connection which, upon physiological grounds, in Man we should expect to find as large and extensive as that of the retina through the optic nerve. It is very remarkable, however, that no such connection of the centres of origin of the auditory nerve with the cerebral peduncle is discoverable.

We obtain, indeed, in the regions of emergence common to the auditory and facial nerves, the most striking appearance of a complete bending round of the *posterior longitudinal fasciculus* into the centres of origin of the auditory nerve at its side (fig. 256, 8, VIII), which in the first instance led me to regard the posterior longitudinal fasciculus as an auditory cord or column. Extremely successful preparations, however, subsequently made from the pons of the Dog by the staining method, showing the most delicate details of structure, have convinced me that the posterior longitudinal fasciculus is only traversed by the central auditory fasciculus, so that it appears precisely as if it curved round, whilst it really descends to the anterior columns of the spinal cord (Stilling).

Stilling indeed already noticed that the straight fibres of the raphé pass into the external roots of the auditory nerve (striæ medullares); by far the greater number, however, have no connection with the crus cerebri, as they can be followed on the other side of the middle line as fibræ arcuatæ in the crus cerebelli.

After all that has been said, we may regard it as certain that

no extensive *immediate* connection of the auditory nerve with the cerebral lobes exists, but that such a connection, the existence of which may be assumed as a necessary physiological truth, can only come to pass *indirectly* through the *cerebellum.*

Amongst such connecting cords sent forth by the cerebellum, we can only suppose that the inferior peduncle of the cerebellum or the medullary velum joining with the frenulum of the corpora quadrigemina may prove to be the one. Should it be hereafter shown that this peduncle—its size corresponding to that of the optic nerve—is the tract connecting the auditory nerve with the cerebrum, the decussation of the tegmentum would have the significance of a *chiasma* of the *auditory sense.*

The origin of the auditory nerve, however, embraces the following sets of fibres, proceeding in part from the above-named nuclei.

In the first place, we must distinguish an *anterior* principal root running through the pons in front of the crus cerebelli, from a *posterior* principal root, which includes the striæ medullares, and embraces the crus cerebelli with its most external fasciculi.

The collected fasciculi of the *anterior* root run with a height of two millimeters, and a breadth of one millimeter, between the corpus restiforme and the ascending root of the fifth, and are composed of decussating and non-decussating fasciculi of origin.

1. The decussating fasciculi are the most internal of those forming the anterior root, and arise apparently from the innermost auditory nucleus of their own side. These fasciculi of origin, however, which, extending transversely from the raphé, traverse the internal auditory nucleus and the fasciculi of the internal division of the cerebellar peduncle of the same side, pass in a twofold form from the internal division of the opposite cerebellar peduncle. In their first mode of running they pass from the crus cerebelli, through the internal auditory nucleus, in a line which can be drawn through the auditory rod of Bergmann, or rather through several ascending *auditory striæ* of J. Engel (and thus down to the inner extremity of the *transverse* striæ medullares), partly superficially in the form of the above-named formations, partly more deeply situated (in front of the genu of the facial

nerve), in order, on the other side of the median line, to reach the auditory nucleus opposite to their origin from the cerebellum. They thus interlace with both posterior longitudinal fasciculi.

In virtue of this course, the fasciculi, *H'*, traversing the *posterior* sections of the internal area of the cerebellar peduncle with the auditory fasciculi, 8^s, interweaving with the *anterior* sections, would form, in fig. 255, at *H*, a continuous tract of decussation through the auditory nucleus, VIII., the whole of which, however, never occurs in one and the same plane of transverse section. A phase of this tract is exhibited in fig. 256, at 8″ VIII.

In their *second* mode of running, the cerebellar fasciculi, without traversing the internal auditory nucleus, pass through the external nucleus directly forwards, and into the fibræ arcuatæ (fig. 255, *a*) which are all placed *in front of* the posterior longitudinal fasciculi, but in the raphé curve round towards the grey floor, and run through the posterior longitudinal fasciculus, and behind it into the opposite internal auditory nucleus. With the rootlets that run towards the median decussation through the external auditory nucleus transversely into the root of the auditory nerve, these still undecussated cerebellar fasciculi form a rectangular trellis-work in the fenestræ of which are contained the transverse sections of the descending fasciculi of the internal division of the cerebellar peduncle (fig. 255, *H*, 257, *S F C*). The innermost fasciculi of the anterior root traverse the ascending fifth nerve, and the lowermost pass into the root, not through the cerebellar peduncle, but immediately in front of it. Stilling, deriving it from the auditory nucleus of the same side, considers this last to be the only mode of origin of the auditory nerve.

The *non-decussating* portions of the anterior root arise—

2. From the *external auditory nucleus* (Clarke, Dean), the large cells of which form a tolerably well-defined and individualized cluster external to the transverse sections, and extend their processes apparently into the root fibres (fig. 255, 8^i). These fasciculi of the root extend themselves beyond the nerve corpuscles into the cerebellum, and indeed, as I have satisfactorily convinced myself, in Man, both through the superior

peduncle, as well as external to it (Clarke, Dean), (fig. 255, on the left side, *B*). The large cells of the external auditory nucleus are continuous, according to Clarke, both with the surrounding transverse sections and the trellis-work.

3. From the transverse sections of the restiform body (fig. 255, *St*).

4. From the *anterior* auditory nucleus (Stilling), which is again the medium of communication with the medulla of the cerebellum (fig. 255, 8^2). To the *posterior* auditory root unite themselves—

5. *Superficial fasciculi,* the *striæ medullares* which cover the internal auditory nucleus and the crus cerebelli. Proceeding from the internal division of the opposite cerebellar peduncle, they pass forwards through fibræ arcuatæ that near the raphé curve backwards and extend through their structure to the surface of the floors of the fourth ventricle.

6. The *deep-lying* fasciculi of the external root cover the peduncle of the cerebellum of the side on which they emerge, but not the grey floor; for although they behave themselves to the side of their origin like the fasciculi of the medullary striæ they do not run back in the raphé quite to the surface of the grey floor. The posterior of these superficial fasciculi traverse the whole of the internal auditory nucleus, extending nearly to the median groove. The anterior fasciculi, however, leave the raphé before reaching the grey floor, so that they form fibræ arcuatæ on the side on which the root emerges, which cut through the anterior angle of the auditory nucleus, and extend backwards in the grey substance of this nucleus close to the internal border of the crus cerebelli. Between the most posterior transverse sections of the internal division of the crus cerebelli they pass outwards, and run with the remaining fasciculi of the posterior root over the restiform body (fig. 257, the fasciculi between x and x^1 and those behind *S F C*).

Another fascicular portion of the external root, lastly, according to the accurate statements of Clarke and Dean, traverses the restiform body instead of encircling it. This portion may not improbably proceed by means of arcuate fasciculi from the opposite internal division of the cerebellar peduncle. Like the auditory nucleus itself, the arcuate fasciculi and radial fibres

connected with it descend as far as to the region of the roots of the vagus (fig. 257, VIII).

The numerous arcuate bands that belong to the central tract of the auditory roots lie behind the transverse fasciculi of the posterior division of the pons, which are connected with the superior olivary body.

The large scattered nerve-corpuscle formation of the posterior division of the pons is continuous with the fibres just mentioned. If these, as Deiters holds, are to be regarded as scattered masses belonging to the motor nuclei of the facial, hypoglossal, vagus, and accessory nerves, their introduction into the auditory tract may be regarded as indicating a central connection of the sound-receiving and sound-producing organ (larynx) within this sphere of reflex action in the posterior tract of the cerebral peduncle.

The relations of the similarly connected scattered masses with the abducens are perhaps, physiologically speaking, not quite obscure, if the reflex rolling outwards of the eyes, that occurs when sounds are heard, is borne in mind.

Transverse sections through the oblongata show in a natural manner the type of a *middle system* which was only artificially transferred by Deiters to the pons, and which is actually a *mixed* system, composed of motor and sensory portions. To it belong the ninth, tenth, and eleventh pairs of cerebral nerves, whilst the twelfth pair occupy the position of an *anterior* (internal) nerve-origin, and the ascending root of the fifth pair that of a *posterior* origin (figs. 257, 258, X, XI, XII, *S*, *G*).

The types of the last two origins are again found separated in the anterior and posterior roots of the spinal cord; the type of the *middle* system, on the other hand, closes with the lowest fasciculi of the root of the eleventh pair of cerebral nerves. The origins of the *median* or *lateral mixed* system of the glossopharyngeal, vagi, and accessory nerves offer so many points in common, that they may be considered together.

The grey floor, in which the greater part of their nuclei of origin are situated, exhibits an elevation below the striæ, indicating the position of the internal auditory nucleus, external to which is the external auditory nucleus with the fasciculi of the

internal division of the crus cerebelli (fig. 257, VIII, *SFC*). These masses gradually and coincidently disappear below the fasciculi passing into the fibræ arcuatæ of the posterior area of the medulla oblongata.

Situated at first immediately by the side of the internal auditory nucleus is a median elevation that Clarke has recently correctly designated the fasciculus (eminentia) teres (fig. 257, x^4—x); for the hypoglossal nuclei never extend as far as the ependyma of the grey floor, but are covered both in the calamus scriptorius, and in front of the central canal, by the *eminentia teres* (fig. 258, where it appears in the form of a dark mass behind XII^1 and XII^2), which is composed of small nerve corpuscles, having a length of 21—30 μ, and a breadth of 6—9 μ, and a large number of fibres. The eminentia teres has a fusiform appendage, the "median nucleus," on its inner side, and near the middle line, composed of the same elements (figs. 257, x^3; 258, XI^3). Both of these clusters, which are to be regarded as nuclei of origin of the lateral system, are thickest beneath the striæ, and becoming attenuated assume a club-shaped form below.

It is requisite to distinguish in transverse sections the *anterior angle* of the grey floor from the auditory nucleus and the eminentia teres; for it is received between the diverging boundary lines of these two masses, and higher up in the medulla oblongata includes in its substance the *two glosso-pharyngeal nuclei* of Clarke, which are inconsiderable clusters of nerve corpuscles that are for the most part fusiform and have a length of 45 μ, and a breadth of 15 μ. The *external* is situated in the apex of the anterior angle, the *internal* about one millimeter further inwards.

At lower planes of section the anterior angle is occupied by the *posterior* nucleus of the vagus (fig. 257, x^1), a mass in which Clarke also distinguishes an internal and an external nucleus.

This cluster of fusiform corpuscles, having a length of 30—45 μ, and a breadth of 12—15 μ, extending towards the point of emergence of the roots, is the upper part of the *vago-accessory nucleus* of Stilling, and, with the *glossopharyngeal nuclei* of Clarke, may be regarded as the *posterior* column of origin of the *mixed lateral system*, the continuation of which in the

spinal cord constitutes the *basis* of the *posterior cornu*. Still higher up, this vagal nucleus becoming confined to the anterior angle of the grey floor (fig. 257), whilst the auditory nucleus and eminentia teres diminish in size, passes forward as the ala cinerea to the plane of the grey floor, and entering the accessory nucleus is situated to the side of, and behind, the central canal (fig. 258, XI[1]). The vago-accessory nucleus contains a number of scattered darkly pigmented nerve corpuscles of nearly equal size, and has on its outer side a cluster of fusiform cells having a length of 21—24 μ, and a thickness of 6 μ, bounded by a peculiar convolute of very fine fibrils, the former becoming visible with the disappearance of the auditory nucleus, and after the closing in of the central canal appearing connected with the commissure enclosed in the bolt (Obex). These fusiform cells extend towards the origin of the root.

Opposite to the vago-accessory nucleus, and enclosed by the transverse sections of the posterior division of the medulla oblongata, is situated the *anterior* column of origin of the *lateral mixed* system (fig. 257 X[2]), in the form of an oblong nucleus lying at a distance of three millimeters from the grey substance of the central cavities, composed of multicaudate nerve corpuscles 60 μ long and 21 μ broad, between which the fibræ arcuatæ of the origin of the posterior column pass through, and are distinctly continuous with their long processes. Deiters, in accordance with his views of the motor fasciculi of the origin of the vagus, has correctly understood the significance of this nucleus, whilst Clarke, in consequence of his misapprehension of the inferior facial nucleus, regards it as a continuation of the motor nucleus of the fifth.

It is important to distinguish it from the more posteriorly and externally situated nuclei of the lateral column, which was included under the cluster formations.

This *anterior nucleus of origin* of the lateral system represents in the medulla oblongata the *processus lateralis* of the anterior cornu of the spinal cord. The former allows the upper, the latter the lowermost, fasciculi of origin of the lateral system to arise from it as the accessory nerve (fig. 261, XI).

An elongated, tolerably close cluster of large fusiform radially

arranged nerve corpuscles, which also appears to belong to the masses of origin of this system, is found attached to the anterior border of the root of the fifth.

The masses of origin of the lateral root system are connected with the crus cerebri (1) through the *fibræ rectæ* of the raphé which penetrate into the fine *fibrous masses* of the *median nuclei* and of the eminentiæ teretes which bend towards the emergence of the roots, and have been described by Deiters as marginal fibres surrounding, but not belonging to, the hypoglossal nuclei (figs. 257, 258, X^4 *R*, XI^3 *R*); (2) through the *fibræ arcuatæ* immediately adjoining the grey floor, which pass from the raphé into the vago-accessory nucleus (Stilling, Schröder, Clarke, Gerlach). Two other prolongations of the crus cerebri in the middle lateral system of the medulla oblongata pass directly into its root fasciculi. They form the first in the enumeration of the *root fasciculi of the lateral mixed system.*

1. The ascending root common to the glossopharyngeal vagus and accessory nerves represents the "solitary fasciculus," already known to Stilling and Lenhossek, that lies beneath the grey floor at the inner border of the cerebellar peduncle, and is applied lower down to the inner border of the posterior column (fig. 257, without lettering; fig. 258, *W*). Its fasciculi proceed from the raphé within the planes of origin of the superior accessory roots, just above the decussation of the pyramids. They probably arise from the pyramids, or from the crusta of the crus cerebri. They form, counting from behind, the second series of the fibræ arcuatæ, and become aggregated towards the transverse sections of the above-mentioned ascending root, which, as soon as it is within the planes of origin of the vagi nerves, receives no further additions from the fibræ arcuatæ. This fasciculus contains, near the border, nerve corpuscles which are for the most part of small size (21—30 μ long, and 9 μ thick), and break it up into very fine sinuous bands that partly gradually pass as rootlets into the accessory and vagal nerves, and partly curve round in considerable numbers above into the glossopharyngeal nerve. This curve is occasioned by the presence of a cluster of the above-named small corpuscles that are

enclosed in a gutter-like fashion by this principal root of the glossopharyngeal nerve (Clarke).

2. *Median roots of the nervus vagus*, which, proceeding from fibræ rectæ of the raphé, pass outwards into the vagus between the hypoglossal roots that arise from thence and the hypoglossal nuclei, in the form of fasciculi limiting the grey floor anteriorly (fig. 257, x x). Other roots of the lateral system probably possess the same mode of origin as the vagus.

3. The roots proceeding from the ganglia of the *posterior column of origin of the lateral system*, including the origins from the above-mentioned nuclei of the glossopharyngeal and vago-accessory nuclei which spring from their nuclei internally to the common ascending root (figs. 257, 258 x^1, xi^1).

4. Root fasciculi proceeding from the *fasciculus teres* to the vagus (Clarke).

5. Root origins from the *gelatinous substance* (fig. 257, *G*) within the *ascending* roots of the fifth, which attach themselves to the nervus vagus and glossopharyngeus as they traverse the roots of the fifth (Clarke).

6. Roots from the anterior columns of origin of the lateral system which I have been able to follow continuously into the glossopharyngeous and vagus (fig. 257, x^2) in almost every transverse section. Running parallel to the principal root towards the grey floor, and curving in front of it, like those of the facial nerve, they form a genu to these two nerves, that differs from the genu of the facial in the absence of any vertical portion.

These portions of the roots, both on account of the size and form of the nerve corpuscles and on account of the lateral position of their nucleus, which corresponds to that of the facial and motor nucleus of the fifth, are to be regarded as motor fasciculi of the lateral system.

7. The *inferior roots* of the accessory nerve spring from the lateral process of the anterior cornu of the spinal cord, as far down as to the lowermost extremity of the decussation of the pyramids, and, indeed, for the most part, not from the cells of the planes of emergence, but by curving, from more distant parts (Stilling, Lenhossek, Clarke, Deiters). The cells of origin

of the accessory nerve below the decussation of the pyramids lie in a plexiform breaking up of the anterior cornu external to the processus lateralis (formatio reticularis), and the roots, which in the upper part were seen to diverge from each other anteriorly, and then traverse the lateral cord transversely (fig. 258, XI; 261, XI), now run in close proximity and parallel to the posterior cornua, without, however, passing through their gelatinous substance. The latter deviation is the rule for the whole accessory tract (Stilling) (fig. 258, XI).

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I will, however, first refer to a connection which occurs between the hypoglossal nuclei and the posterior (reflex) division of the medulla oblongata, which is traversed by the origin of the posterior column and other forms of fibræ arcuatæ.

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enclosed in a gutter-like fashion by this principal root of the glossopharyngeal nerve (Clarke).

2. *Median roots of the nervus vagus*, which, proceeding from fibræ rectæ of the raphé, pass outwards into the vagus between the hypoglossal roots that arise from thence and the hypoglossal nuclei, in the form of fasciculi limiting the grey floor anteriorly (fig. 257, x x). Other roots of the lateral system probably possess the same mode of origin as the vagus.

3. The roots proceeding from the ganglia of the *posterior column of origin of the lateral system*, including the origins from the above-mentioned nuclei of the glossopharyngeal and vago-accessory nuclei which spring from their nuclei internally to the common ascending root (figs. 257, 258 x^1, xi^1).

4. Root fasciculi proceeding from the *fasciculus teres* to the vagus (Clarke).

5. Root origins from the *gelatinous substance* (fig. 257, *G*) within the *ascending* roots of the fifth, which attach themselves to the nervus vagus and glossopharyngeus as they traverse the roots of the fifth (Clarke).

6. Roots from the anterior columns of origin of the lateral system which I have been able to follow continuously into the glossopharyngeous and vagus (fig. 257, x^2) in almost every transverse section. Running parallel to the principal root towards the grey floor, and curving in front of it, like those of the facial nerve, they form a genu to these two nerves, that differs from the genu of the facial in the absence of any vertical portion.

These portions of the roots, both on account of the size and form of the nerve corpuscles and on account of the lateral position of their nucleus, which corresponds to that of the facial and motor nucleus of the fifth, are to be regarded as motor fasciculi of the lateral system.

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at p. 508 of the lateral system, come under the head of the radiating fasciculi of the medulla oblongata described by Lenhossek.

The longitudinal *fibræ rectæ*, connecting the hypoglossal nucleus with the pyramids, appear to be continuous with the *scattered "nuclei of the pyramids"* of Stilling, which are especially developed along the internal border of the pyramids, and which are composed of clusters of nerve corpuscles that agree

Fig. 258.

Fig. 258. Transparent transverse section of the medulla oblongata of Man, immediately below the apex of the calamus scriptorius. *C*, Central canal ; *P*, pyramid ; *O*, inferior olivary body ; *M E*, nucleus of the lateral column, not far distant from its free external surface behind the olivary body ; *S*, region of Rolando's eminence (ascending

with those of the anterior division of the pons. These clusters are immediately connected with disintegrated plexiform portions of the stratum zonale contained in the pyramids; and it would appear, therefore, that the connections of the anterior crus-cerebri tract of the hypoglossus is effected by the *small anterior pons* covering the pyramids.

These fasciculi of the crus-cerebri form a contorted knot-like mass in the hypoglossal nuclei, through which they run to reach the *rootlets* of that nerve. The *central extremity* of the glomerulus projects from the raphé through the *most posterior* fibræ arcuatæ, forming a continuation of the above-described fibræ rectæ. After these fibræ arcuatæ have, as they run along their external border, successively entered each of the two hypoglossal nuclei, and united themselves with the multicaudate nerve corpuscles, they penetrate along the inner border of the nuclei into the hypoglossal rootlets, which for the most part emerge between the pyramids and the olivary bodies, but in part also through the olivary bodies themselves. The fact that such traversing fasciculi not unfrequently terminate abruptly in the interior of the olivary body has led Lenhossek and Schröder v. d. Kolk to adopt the erroneous view of a partial connection of the hypoglossal nerve with the olivary body through a pedunculus olivæ.

All observers—and amongst the most recent, Gerlach—admit also a direct origin for the hypoglossal fasciculi from the crus cerebri through the raphé, the fibres of which, forming the

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root of the fifth); *G*, gelatinous substance, with transverse section of the medulla of the ascending roots of the fifth; *Z*, zonular layer, forming posteriorly the most inferior remains of the restiform body; *H*, posterior column of the medulla oblongata, with the nuclei of the cuneate column (*Cn*) and of the slender fasciculus (*Gr*); *Oe* and *Oi*, external and internal accessory olivary bodies; *R*, raphé; *M F J*, *M F E*, internal and external division of the transverse section of the motor area (anterior and lateral columns); XII^1 and XII^2, internal and external convolute of the hypoglossal nucleus; XII, root of the hypoglossal; XI, root of the accessorius; XI^1, nucleus of the accessory; XI^2, a nucleus of the accessory nerve which is connected with the commissure running in the bolt (Riegel) (*Ob*); *W*, the ascending root of the lateral mixed system; *A S*, fibræ arcuatæ.

innermost fasciculi of the roots, pursue a direction opposed to that of the fibræ arcuatæ, and run with their convexity directed backwards, through the posterior fasciculi of the anterior column (fig. 258, XII).

We cannot, however, be certain that these fasciculi are not interrupted by nerve corpuscles, especially in the raphé. Were they uninterrupted, they would certainly accord with the course of the facial nerve.

A commissure between the two hypoglossal nuclei formed by the decussation of very fine fibres traversing the grey median line behind the anterior column has been described by Gerlach; and Clarke has shown in longitudinal sections a connection between the facialis-abducens nucleus and the hypoglossal nuclei within the grey matter of the central cavities. In regard to such connections, many difficult peculiarities of course are no doubt open to discovery that may prove of high importance for the physiological comprehension of co-ordinated reflex phenomena.

The transverse fasciculi in the posterior division of the medulla oblongata form, above the decussation of the pyramids, counting *from before backwards*, seven orders or arrangements, which are continuous with the following different parts: (1) with the corpora restiformia; (2) with the posterior column (cuneate and slender fasciculi); (3) with the internal division of the crus cerebelli; (4) with the root of the auditory nerve; (5) with the ascending root of the *lateral mixed* system; (6) with the glossopharyngeal and vago-accessorius nuclei; (7) with the hypoglossal nuclei.

5. The Cerebellum.

The centre situated behind the peduncle of the cerebrum—the cerebellum—the addition of which to the just-described division of the projection system confers upon it its peculiar characteristics, is far more closely proportional in point of size to the cerebral lobes than is the ganglia of the tegmentum, or the posterior tract of the peduncle. This relative development affects essentially the lateral portions or hemispheres of the cerebellum, whilst the vermiform process preponderates in the lower forms of brain. Within these hemispheres, however it is the interior region of their upper surface, the alæ of the

central lobe and the quadrilateral lobes, that attain their greatest development in the cerebellum of Man (Huschke). The cerebellum includes three different forms of grey matter: (1) The *cortex of the cerebellum*, the most extensive and largest of its centres; (2) the *dentated nuclei*, in the medulla of the hemispheres; and (3) the *roof nuclei* (Dachkerne) of Stilling, in the medulla of the vermiform process.

Fig. 259.

Fig. 259. Transparent section from the cortex of the cerebellum of Man. 1*a*, External portion of the pure grey layer; 1*b*, internal portion of the pure grey layer, with fusiform cells and fibræ arcuatæ; 2, the layers of Purkinje's cells; 3, the granule layers; *m*, medullary lamina.

1. *The cortex of the cerebellum.*—Obersteiner has found that the three layers of the cerebellar cortex already recognized by Purkinje are argumented in the fœtus and in the cerebellum of the new-born infant by an outermost layer of extremely closely compressed formative cells, which at a later period

become elongated and spindle-shaped, and change into the connective-tissue fibres of the innermost layer of the pia mater. This connective-tissue investment contains at the same time the thickened triangular points of attachment of the radiating supporting trabeculæ, resembling those seen in the retina, which have been described by E. Schulze, Bergmann, and Deiters, and which Obersteiner followed to their connection with the reticular stroma, as far as to the inner margin of the pure grey layers, under most favourable conditions of isolation, in the cortex of a cerebellum that appeared as though it had been pencilled out, in consequence of an atrophic process of encephalitis.

The remaining separable layers are (1) the *pure grey layer*, which is the most external; (2) the middle *thin layer of large cells of Purkinje*; and (3) the internal *greyish-red or granule layer* (fig. 259, 1*a*, 1*b*, 2, 3). The external layer contains a large proportion of a reticulo-molecular matrix, precisely similar to the connective-tissue matrix of the cortex cerebri, which Stilling alone regards as a felt composed of the finest ramifications of the ganglion-cell processes. In addition to what appear to be free nuclei of the connective tissue, small triangular (pastille-shaped) and fusiform nerve corpuscles are imbedded, measuring from 6 to 10 μ. On account of the fluidity of their protoplasm, it is often more difficult than in the cerebral cortex to satisfy one's self of their being really nerve corpuscles.

At the inner margin of this layer, around the furrow between every pair of convolutions, these small elements are elongated and fusiform, and are parallel and in connection with a layer of transverse finely varicose nerve tubes (fig. 259, 1*b*), which certainly have the appearance of being "fibræ propriæ" of the cerebellar cortex. We cannot, however, regard them as such with absolute certainty, because, as we shall show hereafter, the processes of the adjoining large cells also extend transversely around the sulci, and might produce the appearances in question, though if so they would be undoubtedly connected with the processes of the small cells.

The middle layer of the cerebellar cortex contains the large corpuscles of Purkinje, arranged in a single layer (fig. 259, 2).

The thick body of these elements, measuring from 60 to 70 μ in length, and from 20 to 30 μ in breadth, is most frequently vesicularly expanded towards the granule layers internally, and is there without processes, whilst the large processes directed outwards are always visible. According to Kölliker, Deiters, Koschewnikoff, and Hadlich, each cell gives off on its inner aspect only a single process, which the three last observers maintain is medullated and unbranched, whilst Stilling considers there are several branches which immediately divide in a plexiform manner in the granule layer, and, according to Gerlach, unite with the granules. Hadlich attributes the connection with the granules to the finest ramifications of the thick finely striated processes which run into the pure grey layer, the minutest filaments of which curving back, as already stated by Obersteiner, near the surface of the cerebellar cortex, join a plexus which is in direct connection with the granules. He adduces also, as a ground of probability for this, the broad fact that at the level of the lamellæ of convolution the closest approximation of the cells of Purkinje coincides with the greatest breadth of the granule layer; and again, that around the sulci the most sparing distribution of the former occurs, with the greatest attenuation of the latter. According to Obersteiner, the cells of Purkinje spread forth their numerous antler-like branches in a single plane, so that they do not each form a brush or cone of fibrils, but resemble the ribs of a leaf, whence the laminar structure of the medulla of the cerebellum would also be expressed in the structure of the cortex. Lastly, Obersteiner and Hadlich have found that the remarkable transverse divergence of the large primary processes of the cells of Purkinje, by virtue of which they extend parallel to the surface of the cortex in opposition to the similar processes of other cells which run radially to the surface, represent a mode of branching that occurs only in those portions of the cortex that surround the sulci.

The large cells appear to me to be invested by a loose hyaline sheath which is extended for a little distance along the larger processes. Obersteiner regards it as a plexus of supporting fibres loosely investing the cell. The internal layer, which was already recognized by Purkinje, and has been subjected to a

careful investigation by Gerlach, presents the closest similarity to the granule layers found in the olfactory lobes. Its elements, on account of the protoplasm surrounding them being extraordinarily delicate and destructible, appear in the form of very minute naked granules, measuring 6 μ, respecting which a threefold interpretation has been given. Gerlach and Kölliker believed that they saw in them a cluster of elements belonging to the connective substance, which Gerlach nevertheless allowed to be enclosed by the internally directed processes of the large nerve cells. Henle and Merkel look upon them as lymph corpuscles. Stilling regards them as an extremely small variety of multipolar nerve corpuscles, connected with each other in a reticular manner. Their protoplasm, which is often enough distinctly marked, and gives off several processes that do not very frequently branch (fig. 235, *e*), is sharply defined, and of a hyaline clearness in the cerebellum of the newly born infant (where they have been shown to me by my colleague, M. Fries, of Vernek), in consequence of which these elements strongly resemble the inner granules of the retina.

The *medulla* of the cerebellum contains, in the medullated laminæ of the convolutions, numerous granular elements which, in part at least, are emissaries of the granule layer. A considerable proportion of them, however, are to be regarded as connective-tissue elements. I have arrived at a positive conclusion on this point on account of the pathological changes to which I have referred at p. 385, and which repeat themselves in the medulla of the cerebellum.

According to Stilling, the fibres of the medulla of the cerebellum, in opposition to the conditions requisite for isolated conduction, are everywhere connected with each other in a plexiform manner. This course, which has not been corroborated by any other observer, can only have been supposed to occur by confounding a connective-tissue reticulum with the nervous elements, owing to that haziness of the image with which the remains of the altered medulla cover and conceal the arrangement of the elements in sectional preparations that have not been rendered thoroughly transparent. Stilling himself raises an important objection to his own statement when he describes, notwithstanding the supposed connection

on every side, the distinct lamellation of the medulla of the cerebellum when its fibres are separated.

2. The *dentated nuclei*, discovered by Vieussens, form inferior grey medullated, and in Man contorted, laminæ, having a thickness of 0·3 of a millimeter, lying near that surface of the cerebellum which overlaps the fourth ventricle, the contained medullary substance of which enters it by a hilus directed downwards and inwards. Their fine dentations exhibit in Man the most remarkable similarity to the inferior olivary body, which they also resemble in the cellular elements they contain, which are 30 μ long, and 12 μ thick. I distinguish the presence also, in Man, of *secondary dentated nuclei*, which are of smaller size, but are composed of a thicker grey lamina, measuring 0·6 of a millimeter, situated somewhat below and in front of the former, and containing larger elements (having a long diameter of 45 μ, and a breadth of 15 μ) Their sinuosities are less fine and close than the principal dentated nuclei, and the continuity of the curves is frequently interrupted by the passage through them of strong medullary fasciculi. In Mammals (as in the Quadrumana, fig. 255, *D D*), the nucleus no longer possesses the beautifully marked appearance, the delicate curvatures, of that of Man, but is distended by the introduction of a considerable quantity of connective tissue into its interior, and forms a simple mass of grey substance, with a sinuous outline.

3. The *roof nuclei* (Dachkerne), discovered by Stilling, are two convex and, when seen from above, rhombic masses, which in the cerebellum of Man are situated below the central lobule of the superior vermiform process, and have a length and breadth of about five millimeters, and a height of two millimeters. Their connections may be exposed by careful dissection; and they are then found to be separated from one another by a thin median medullary layer, and to be traversed by a considerable quantity of medullary substance. They contain long slender nerve cells, which are provided with thick processes, and have a length of 60 μ, and a thickness of 15 μ or more, corresponding therefore in size with those in the external auditory nucleus (fig. 255, *T*).

Our knowledge of the course of the *medullary fibres* of the

cerebellum is still in a very imperfect and fragmentary state. Stilling, in the part referring to it in his great work, has not entered into its description beyond giving an account of the uvula and of the central lobule. We must undoubtedly admit the existence of medullary systems in the cerebellum, which arise and terminate in this centre, and, as *fibræ propriæ*, contrast with the peduncles, which run out and are prolonged into certain parts of the trunk.

1. *Fibræ propriæ.* Burdach, Arnold, and, from the examination of sections, Stilling, have described the *common* fibræ propriæ as *garland-like* fasciculi (arranged in delicate lamellæ) extending along the inner surface of the cortex, from convolution to convolution. Stilling also describes still more extensive systems of *special fibræ propriæ*, which serve to connect more remote portions of the cerebellar cortex with each other. His description includes that of the symmetrical pairs of fasciculi belonging to this system, running near the middle line, to which he has applied the term *median fasciculi.* An anterior division of the same runs symmetrically on either side, from the most anterior portions of the superior vermiform process, straight beneath the roof-nucleus to the lobules of the inferior vermiform process; that is to say, from the uvula to the nodulus. Another and also symmetrical division, consisting of stronger median fasciculi, encloses the former concentrically, and runs, forming an arch directed in the first instance with its convexity towards the superior vermiform process, but subsequently backwards, which extends from the most anterior convolutions of the superior vermiform process to the most remote, that is to say, to the most anterior, convolutions of the inferior vermiform process. Moreover, a variously developed proportion of *transverse commissural fasciculi* is found in the cerebellum, which, crossing the middle line, connect corresponding opposite and symmetrical regions of the cerebellum, exactly in the same manner as is effected in the cerebrum by the trabecular system of the corpus callosum.

2. *The arms or brachia of the cerebellum.* Of the brachia of the cerebellum the processus ad pontem and a great part at least of the restiform body take a simple course. The points of decussation of their fasciculi, as has been already

described, are external to the cerebellum. They remain in the substance of the cerebellum itself up to the point where they penetrate into the cortex, on the same side as that on which they enter, though, no doubt, so far as they also penetrate into the most central portions they are directed inwards, and are consequently so disposed as readily to give rise to an erroneous impression of running towards a point of decussation.

The relations of the prolongations of the brachia of the cerebellum to one another is determined by the disposition of the grey substance with which they unite in the cerebellum. The *processus ad pontem* and the *corpora restiformia* are only connected with the cortex; the superior peduncle, however, is previously connected with the *nucleus dentatus*, and the inner division of the cerebellar peduncle with the *roof nuclei* of the cerebellum. Now, since the cortex is the most externally situated mass of grey substance, whilst the dentated nucleus lies in the middle of the medullary layer between it and the internally situated roof nuclei, these arms are so disposed in the medulla of the cerebellum, that the processus ad pontem and corpus restiforme form the *most external*, the superior peduncle the *middle*, and the so-called internal division the *innermost* mass of its layers (fig. 255, *Br*, *St*, *B*, *H*').

The nucleus dentatus, moreover, is immediately covered by a smooth separable layer of the restiform body, which fills up the furrows of its surface, and the fibres of which perhaps also enter into connection with its nerve corpuscles.

The *superior peduncle*, which has already decussated in the substance of the tegmentum, like the external arms, runs straight in the cerebellum, and reaches the hilus of the *nucleus dentatus* (Gratiolet), within which it diverges to meet the nerve corpuscles radiating towards them. As far as to the hilus, however, it does not present a pure and unmixed sectional area, but just as in its free course it is already traversed by fasciculi of the fifth, and further downwards by those of the auditory nerves, so it is here freely traversed by other fasciculi of the medulla of the cerebellum, especially by the inner division of the cerebellar peduncle. This *internal* column of the crus cerebelli appears to pursue a double course. Its internal fasciculi in part enter straightway into the roof-nucleus of the

corresponding side, but in part, at least, following the sinuosities of its upper borders, into that of the opposite side. They thus pass through a slender medullary median layer, a kind of raphé, which extends between the roof-nuclei, and which being traversed by antero-posterior medullary fibres (median fasciculi of Stilling) appears very opaque. In this raphé they decussate, and near the lower border enter into the opposite roof-nucleus. In their further course they must reach the medulla of the inferior vermiform process, by the commissural fibres of which they must be brought into connection with all the lobes of the inferior cortical region of the hemispheres. The most anterior of these commissures is the *posterior medullary velum*, which joins the cortex of the *flocculus* by means of a fasciculus of the peduncle of the latter.

The second fasciculus of the peduncle of the flocculus passes, as is well known, over the auditory nerve, to run up to the lateral wall of the fourth ventricle, and still higher up to return again into the cerebellum with the crus cerebelli (fig. 255, *F*).

The *external* fasciculi of the internal column of the crus cerebelli (fig. 255, H^2), after they have passed through the superior peduncle, enter without decussating into the medulla of the cerebellum, leaving the roof-nuclei on their inner side.

The fasciculi of the *internal column* at all events diverge in so many directions from each other in the cerebellum, that we may reasonably admit their connection with all parts of the cortex of the cerebellum (as is also true of the processus ad pontem and of the restiform body).

The course which the tract representing the *auditory nerve* pursues in the cerebellum is still imperfectly ascertained in regard to its decussation. The *non-decussating* fasciculi of the anterior *auditory root* (fig. 255, 8^4, and the corresponding fasciculus on the left), escape the decussation in the roof-nuclei by passing directly through the superior peduncle and nucleus dentatus. But whether also the portions of the *anterior* and of the *posterior* auditory roots, that have already undergone *decussation* in the posterior division of the pons, remain in that half of the cerebellum they have once reached, where they are no longer distinguishable from the fasciculi proceeding from the

transverse section of the internal column of the crus cerebelli, cannot as yet be decided. Speaking broadly, we do not know whether all the fasciculi of the internal column of the crus cerebelli represent portions of the auditory tract, or not. The decussation between the roof nuclei necessitates a re-decussation (?) under all circumstances, because the transverse sections of the internal division of the crus cerebelli run below into the fibræ arcuatæ.

The view expressed by Kölliker and Deiters, that the cerebellum, regarded as a whole, must represent a loop or sling, the curves and sinuosities of which establish very indirect connections between the cerebrum and the nerve-roots, is scarcely supported more strongly by any other fact than by this, viz., that the auditory nerve, which is so intimately connected with the functional activity of the lobes of the cerebrum, is in all probability, by its immediate connections entirely lost in the cerebellum.

The relations probably existing between the cerebellum and the muscular sense postulate the looping of other tracts running in the cerebellum towards the cerebrum. In truth, it can only represent an important station for the conduction of these impressions, because its predominant position in regard to consciousness, as in other sensorial regions, in accordance with Wundt's happy expression, also conditions the signals of these sensations reaching the cerebrum. Any attempt to illuminate the chaos of possible combinations of the outrunners of the cerebellum in their course through its grey substance would at present embrace more suppositions than matters of fact, and therefore cannot be entered upon in an account properly based on morphology. In a morphological point of view, we can only refer to two theories of the mode of looping, supported by facts. One of them lies in the actual looping, observed by Obersteiner and Hadlich, of the ramifications of the processes of the large nerve cells of Purkinje; the second is founded on the very peculiar form of these nerve cells.

The nerve cells of Purkinje are namely, in a morphological sense, bipolar. Their internal and external extremities are the rudiments of two different types of nerve corpuscles. If we could divide a nerve corpuscle of Purkinje into two halves.

and connect each of them with another similar half, so as again to form one whole, the distended base, directed towards the granules of the commonly called "flask-shaped" body with its (probably) *single* process, would by its duplication represent one of those vesicular forms, poor in processes, that are connected with the *sensory* roots in the interspinal ganglia, in the Gasserian ganglia, and in the descending roots of the fifth (see p. 448). The half which passes into the neck of the flask, that is to say, by gradual attenuation into the thick processes turned towards the pure grey layer, would, on the other hand, by its duplication, represent one of the slender forms, rich in thick processes, that form the nuclei of origin of all *motor* roots.

The nerve cells of Purkinje would consequently (if the statements of Deiters, Koschewnikow, and Hadlich, in regard to their unbranched connection with one axis-cylinder be correct) be connected by that extremity which is formed on the type of a sensory cell, with one *centripetally conducting fibre*, and through its branched extremity, constructed on the type of a motor cell, with several *centrifugally conducting* fibres. The circumstance that the smaller (poorer in fibres) restiform body passes into the posterior column of the spinal cord, whilst the far larger (more abundantly fibrous) processus ad pontem is connected with the crusta, which, on account of its origin from the lenticular and caudate nuclei, is motor, demonstrates that in general the *proportionate size* of these cerebellar arms corresponds with the *relative numbers* of these two forms of cell processes, and supports the view that in each of the cells of Purkinje we have a nodal point which effects the looping of two tracts having different significance.

6. The Structure of the Transitional Region between the Medulla and Spinal Cord.

In the formation of the anterior and posterior divisions of the medulla oblongata, the double nature of the cerebral peduncle, which had been foreshadowed by the separation of the chief groups of cerebral ganglia, and had become fairly

apparent in the crusta and tegmentum of the crus cerebri, was still clearly expressed.

The *organization of the crus cerebri* had still superadded to it an appendage, the *crus cerebelli*, by the breaking up of which into its constituent fasciculi, in the interior of the medulla oblongata, on the one hand, the most essential portion of the system of arcuate fasciculi, and upon the other the compact grey matter forming the olivary bodies and the scattered grey formations, were introduced into the peduncular organization.

The most essential differences between the organization of this segment of the spinal cord and that of the medulla oblongata consists in four points:—

(1) Whilst the medulla oblongata consists of a prolongation of the *anterior* and *posterior* tract of the crus cerebri, and whilst (2) an additamentum or third tract is found in the crus cerebelli, the transverse section of the spinal cord forms a symmetrical *homogeneous* and continuous *medullary investment* in which the *threefold* mode of origin of the medulla oblongata, as well as the *double* nature of the cerebellar penduncle, is entirely lost. (3) Whilst in the upper half of the oblongata the grey matter of the central cavities is represented by the broad unfolding and expansion of the floor of the fourth ventricle, the motor and sensory nuclei of origin being developed *side by side* as *internal* and *external* masses, we find the organization of the spinal cord disposed around a narrow enclosed cavity, the central canal, in relation to which the motor and sensory grey nuclei of origin are arranged in an *antero-posterior* direction *before* and *behind* each other. (4) The so modified grey matter of the central cavity, in opposition to the variously formed and manifold grey substances of the medulla oblongata, constitutes the single and uniform ganglionic substance of the spinal cord.

These differences are abolished by two principal *morphological processes;* namely, by the closing in of the central canal, occasioned by the formation of the posterior columns, which occurs in the upper half of the medulla oblongata, and by the *decussation of the pyramids*, which occurs in the lower half.

1. *The inclusion of the central canal.* Whilst the fasciculi of the restiform body (*M F C*), constituting the external division

of the cerebellar peduncle, progressively break up below the point where the floor of the fourth ventricle is of the greatest width (fig. 257) into the fibræ arcuatæ, which, after traversing the olivary bodies (p. 470 *et seq.*), reappear upon the opposite side, situated internally to the restiform bodies, in the form of the slender and cuneate fasciculi (posterior column), the restiform body must evidently, in consequence of the passage of its fasciculi into the opposite posterior column, progressively diminish in size, whilst the medullary masses bounding the posterior column on the inner side augment in the same proportion. But if in a given area a certain amount is continuously detached from one side, and equally continuously applied to the opposite, this area must be transposed in the direction of the additions it receives. The transverse section of the cerebellar peduncle *diminishing* in bulk *externally*, and *augmenting internally*, must consequently approximate the median line. As a result of this, it must press upon, and displace inwards, the external column forming the sensory division of the grey floor of the fourth ventricle bounding its internal portion, which appears above as the auditory, but below as the vagal, nucleus. Thus it will progressively deepen the floor of the fourth ventricle; and at a lower plane these grey masses, instead of being external to the *hypoglossal nucleus* (fig. 257), become *posterior* to it (fig. 258); and, being continuously pressed inwards, firstly, the inner surfaces of what are now called the *posterior columns* of the grey substance, and subsequently the inner surfaces of the *posterior* columns, continuously increasing upon their inner side, will at length come into contact. This contact of the symmetrically arranged grey matter leads to fusion with *inclusion of the central canal*.

Between the two posterior columns, however, the posterior fissure of the medulla oblongata is formed. And, in this respect, in this direction it approximates to the form of the spinal c[redacted] (fig. 258, *C*). This approximation appears far more remark[redacted] at the same time it be considered that the form of [redacted] nucleus of the spinal cord, apart from the bilater[redacted] of its masses, already pre-exists in the medulla o[redacted]

The median nuclei of the hypoglossal nerve

the translation of the remote medullary masses of the cerebellar peduncle, continue to run undisturbed into the inner portions of the anterior cornua of the spinal cord. Below the level of the internal accessory olivary bodies this mass gives off no longer hypoglossal roots, but anterior roots of the first pair of cervical nerves (Stilling). The processus lateralis of the anterior cornu is likewise already present (as the anterior tract of origin of the lateral system of roots) in the medulla oblongata. In the progressively diminishing diameter of the descending central peduncle it however no longer finds space for an independent course so remote from the anterior cornu, and consequently fuses with this at the level of the inferior roots of the accessory nerve.

On the other hand, the posterior cornu already appears in the medulla oblongata as a continuous and circumscribed mass.

In the spinal cord it consists of the *caput;* of the *cervix,* which is essentially composed of the traversing posterior nerve roots; and of the *triangular base,* which is fused with the remaining nuclear portion of the spinal cord, and which Goll has designated the *cervical triangle* of the posterior cornu. The *nucleus of the vagus,* the anterior external angle of the grey matter, corresponds exactly to this cervical triangle. If we now take into consideration that the *caput* of the *posterior cornu* is already present in the medulla oblongata as the *gelatinous substance* which envelopes the ascending roots of the fifth, and that this is subsequently traversed by the roots of the vagus entering at the apex of the triangle, which is prolonged towards them (vagal nucleus), the *vagal roots* between the above-named caput of the posterior cornu and the latter mass as its *base* will represent the *cervix* of the *posterior cornu.* This completed posterior cornu of the medulla oblongata is only turned *forwards* instead of, as in the spinal cord, *backwards* and outwards.

If now the vagus, after coalescing with its nucleus, like this nucleus, turns inwards, the gelatinous substance (*G*) must be displaced backwards, and the whole formation of the posterior cornu assume gradually a transverse position, as obviously occurs in the region of the lower half of the medulla oblongata in regard to the posterior roots replacing the vagus. (Fig. 261,

on the left side.) It now only depends upon the breadth of the posterior columns situated between the posterior cornua whether the radii of the posterior cornua moving in the area of the circle formed by the transverse section of the medulla oblongata, can accomplish the approximation found in the cord

Fig. 260.

Fig. 260. Transparent transverse section of the lower half of the medulla oblongata of Man, at the level of the upper part of the decussation of the pyramids. *C*, central canal; *P*, internal and median, and *P'*, external fasciculi of the transverse section of the pyramids; *G*, gelatinous substance in the tuber cinereum of Rolando; *H*, posterior column; *Cn*, nucleus of the fasciculus cuneatus; *Gr*, nucleus of the fasciculus gracilis; *Oi*, internal accessory nucleus; XII, roots of the hypoglossal nerve; *D*, decussation of the external fasciculi of the pyramids which at *H* curve round the tissue adjoining the central canal to reach the funiculi graciles and cuneati; *AA*, fibræ arcuatæ which are continuous with the tissue around the posterior columns, but not with the pyramids; *V*, the anterior column.

to the third radius formed by the posterior fissure. And now, because (figs. 258, 260, 261) the great breadth of the posterior columns above depends, not on the size of its fasciculi, but upon the presence of the grey masses associated with the

nuclei of the slender and cuneate fasciculi, the posterior cornu reaches the position in the spinal masses from the cord it subsequently retains, by the elimination of these posterior columns which remain imbedded in them only as far as to the completion of their origin by the additions they receive from the pyramids.

Coincidently, however, with the difference in the form of the grey substance of the central cavities, which takes place between the medulla oblongata and the spinal cord, and with the *exhaustion of the corpus restiforme*, the *peduncle of the cerebellum ceases to exist*, becoming continuous with the formation of the posterior column; and because, with the conclusion of this process, the system of the *fibræ arcuatæ*, by which it is accomplished, *disappears*, so do the formations of the olivary nuclei and the scattered formations proper to the medulla oblongata, continuous with the fibræ arcuatæ, also disappear. The formation of the posterior column, however, conditions the inclosure of the central canal, so that it is impossible to consider the two processes separately.

Thus, after the closure of the central canal, the area of the transverse section of the medulla oblongata presents the following segments:—

(1) The pyramids (*P*) forming a continuation of the crusta, and still large and complete, lying near the median line. (2) The outer portion of the posterior tract of the peduncle, forming the continuation of the tegmentum of the crus, and destined to pass directly into the antero-lateral column of the spinal cord (from *Oi* to *G*). Behind this runs the triple formation of the posterior column. (3) Adjoining the antero-lateral column of the posterior division of the medulla oblongata, the grey tubercle of Rolando projects, shimmering through its medullary investment as the grey caput of the posterior cornu, which here attains its greatest development. Partly in its interior, and partly surrounding it, the transverse sections of the ascending roots of the fifth nerve, springing from a still lower plane, may be recognized. (4) Behind the tubercle of Rolando, the *triangular nucleus* of the fasciculus cuneatus; and (5) internal to it, near the posterior fissure, the *clavate nucleus* of the *fasciculus gracilis*, enclosed in the posterior columns,

which formations, like the tuberculum cinereum (fig. 258), project outwardly upon the surface.

2. *The decussation of the pyramids.* Although the double nature of the cerebral peduncle still persists within this formation, owing to the presence of the pyramids, the organization is coming to an end by two methods.

In the first place, the origin of the posterior columns of the spinal cord is completed by the external fasciculi of the pyramids (fig. 260, P^1) penetrating internally behind the middle and internal fasciculi of the pyramids, in delicate tracts, extending to the raphé (*D*), in which they decussate, and as a kind of inferior and posterior system of fibræ arcuatæ, curve immediately round the circumference of the central canal in order to pass into the posterior column of the spinal cord. This is the *superior finely fasciculated, sensory decussation of the pyramids.* Clarke, Luys, and Deiters long ago recognized that the posterior columns participate in the decussation of the pyramids.

The origin of the here prolonged external fasciculi of the crusta from definite parts of the lobes of the cerebrum, has already been discussed at p. 409. Deiters also observes that the fasciculi of the crus cerebri are prolonged without alteration of position into the pyramids, and that we must therefore consider the most external fasciculi of the pyramids to be identical with the most external fasciculi of the crusta.

The external fasciculi of the pyramids, however, it is obvious, by that decussation, not only pass into the posterior column of the spinal cord, but also enter into connection with the portions of the posterior roots of the first pair of cervical nerves arising in the planes of decussation, so that these nerves may not be excluded from the decussation occurring in the pyramids.

At the above-mentioned planes of origin, the curves formed by the fasciculi of the posterior columns proceeding from the pyramids are surrounded by the lowermost remains of such fibræ arcuatæ (fig. 260, *AA*), as belong to the above-described cerebellar origins of the posterior column, from which they are distinguished by their more posterior position, their connection with the broad region of decussation (*D*), their thicker calibre, and the circumstance that there is no

grey matter between them and the transverse sections of the posterior division of the medulla oblongata. This juxtaposition shows that there is only an ideal limit between the region of interlacement of the oblongata through the cerebellum and its inferior transitional formation.

The complete cessation of the double tracts of the cerebral peduncle occurs just below the superior decussation of the pyramids, and takes place immediately in the territory of origin of the first and second pairs of cervical nerves, in the form of the *inferior coarsely fasciculated or motor decussation of the pyramids.*

Fig. 261.

Fig. 261. Transparent transverse section of the medulla oblongata of Man, at the level of the inferior decussation of the pyramids; *C*, central canal; *P*, the pyramids in the act of decussation; *VL*, the anterior column and the lateral column; *D*, the decussation of the pyramids; *G*, the caput of the posterior cornu (tuberculum cinereum) which posteriorly discharges itself into a nucleus of the fasciculus cuneatus; *H*, the posterior column; *Cn*, the anterior horn of grey matter; XI, (white) inferior radicl fibres of the accessory nerve; XI, (marked black on the left side in the anterior cornu) transverse sections of curving roots of the accessory nerve.

To it belongs the greatest proportion of the areas of the pyramids, as seen in transverse section, which are about to pass across the median line by broad decussating fasciculi (fig. 261, *D*), and to enter the lateral column of the opposite side. This passage of the pyramids into the lateral column occurs, as Clarke and Lenhossek have stated, without interruption of the fasciculi by grey matter. The fasciculi of the lateral column, which likewise pursuing a transverse course first emerge from the decussation of the pyramid, interlace with the fine transverse sectional areas of other already descending fasciculi of the lateral column as a *formatio reticularis* which first disappears in the uppermost portion of the cervical region of the spinal cord (Stilling, Clarke, and Deiters).

This formatio reticularis moreover includes, in deep-lying sectional planes, numerous large nerve corpuscles, which, however, as Stilling, Lenhossek, and Clarke have pointed out, are only cells of origin of the accessory nerve. The formatio reticularis in Man, however, apparently does not contain, as Deiters maintains, such an accumulation of grey matter as is adequate for the termination of so large a formation as that of the inferior decussating fasciculi of the pyramids. It must be conceded to Deiters that the decussation of the pyramids of Mammals, to which he refers as furnishing more striking evidence in favour of his explanation, exhibits far more the appearance of sufficiency of grey substance in the plexiform formation, for the interruption of all the fibres of the pyramids, than in Man. But the fact that, with very small pyramids, more grey matter can be observed in the medulla oblongata of Mammals, than is present in Man, with his strong pyramids, demonstrates that the two formations are not mutually related. It is rather the considerable development of grey connective substance at this point, by which the brain of Mammals generally is distinguished from that of Man, that really produces the appearances in the medulla oblongata of the Calf and of the Cat which favour the view of Deiters.

The diminution in calibre of the far finer fibres of the pyramids, as compared with the sections of those of the lateral columns of the spinal cord, which favours the view of Deiters,

that an interruption takes place by means of nerve corpuscles, must nevertheless take place in the continuity of the fibres. Clarke and Lenhossek believe they are able to corroborate the view of Burdach, that the pyramids, besides decussating in the lateral columns, are also directly continued into a definite part of the anterior columns of the spinal cord (Burdach's fundamental fasciculus of the pyramids), whilst Stilling and Deiters are unable to perceive any such continuation of the pyramids.

As in the sensory decussation of the pyramids the posterior nerve roots originating at the same level were represented, so Clarke points out that the fasciculi proceeding from the inferior decussation of the pyramids into the anterior cornu of the grey substance represent the anterior roots of the nerves arising at the same level. With the continuation of the most inferior decussating fasciculi of the pyramids into the lateral column of the projection system, both in regard to structure and the arrangement of its grey matter, the type of the spinal cord is attained. And inasmuch as the fasciculi of the lateral column do not participate in the decussation in the anterior commissure of the spinal cord, they do not experience, between their pyramidal course and the passage into the anterior roots, any re-decussation, and are clearly enough adapted for the further conduction of the crossed influence of the cerebral lobes upon the musculature.*

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* At the conclusion of the preceding account of the structure of the cerebrum, it becomes a pleasant duty on my part to express my thanks for the intelligent artistic co-operation of Dr. Carl Heitzmann and of Mr. Adolf Göhre, of Vienna, of whom the former has carefully drawn to nature figs. 230—237, 239, 240, 243—246 and 259, whilst the latter has executed on wood the remaining still more numerous drawings.

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CHAPTER XXXII.

THE SYMPATHETIC SYSTEM OF NERVES.

By Dr. SIGMUND MAYER.

THE so-called sympathetic or vegetative nervous system is widely distributed throughout the animal body, especially in those organs in which the functions of reproduction and of organic life are combined, and in that structure to which the term of sympathetic cord or trunk has been applied. The uniform and regular segmentation that occurs in the cerebro-spinal system is less clearly marked in the sympathetic system, the principal trunk with its successive ganglia alone exhibiting a regular type. Elsewhere the cells and fibres of the sympathetic are more or less irregularly distributed through the body, supplying for the most part the complex systems of the vegetative and generative organs. Whilst the cells of the cerebro-spinal organs exert an influence through the agency of the cerebral and spinal nerves on both transversely striated and on smooth muscular fibres, the action of the nerve cells of the sympathetic on striated muscle has only been demonstrated in Mammals in the case of the heart.

It was formerly much discussed whether the sympathetic nervous system was an altogether independent formation, or was an appendage of the cerebro-spinal system. It is now recognized, however, that such a discussion is profitless; for in view of the free interchange of fibres between the sympathetic and the cerebro-spinal system of nerves, it is obvious that the most intimate connection exists between the two. Both systems, morever, may be regarded as constituting an organization with the same

except that in the cerebro-spinal system the nerve cells are accumulated into large masses, and the connections between the several segments are effected by fibres which do not stray from the region of the central organ, and which preserve the character of the central fibres, whilst in the sympathetic the cells are more separated, and their connections, both amongst themselves and with the cells of the cerebro-spinal system, are established by peripheric nerve fibres. In the cerebro-spinal medullary system the principle of the centralisation of the elements is represented, whilst in the sympathetic system it is rather decentralisation which is the essential feature.

The medullary substance of the sympathetic, like that of the brain and spinal cord, is composed of cells and fibres, and in both situations the fibres arise from the cells.

The peculiarities distinguishing these two elements of the sympathetic nervous system will here be carefully considered; whilst, for their general characters, the reader is referred to the third chapter of this work.

The ganglion cells of the sympathetic are partly united into large groups, to form the so-called ganglia or nerve-knots, and are partly intercalated in the course of the nerve trunks, or are distributed in a scattered manner in the various organs.

The nerve-knots or ganglia of the sympathetic are provided with an investing sheath of connective tissue, which gives off processes that penetrate between the several cells, and form as it were a separate capsule to each. The connective tissue consequently constitutes a trellis-work, the interspaces of which contain the nerve cells; it at the same time supports the bloodvessels. Each ganglion possesses an afferent and an efferent nerve, the fibres of which pursue various courses within the ganglion, one portion running from the periphery to the cerebro-spinal centre, and another in the opposite direction, though as yet no characteristic mark has been discovered by which the one can be distinguished from the other. The nerve cells are imbedded in a confused mass of fibres, so that an insight into the mode of connection between the cells and fibres can only be obtained from careful investigation. Cells are often met with distributed in the course of the smaller

trunks, and indiscriminately near their centre or their border.

The cells of the sympathetic system exhibit the essential features of other nerve cells, such as have been described in the third chapter of this work, but they present, in addition, a few peculiarities which permit them to be distinguished from the central cells of the cerebro-spinal organs. And just as the nerve cells of different regions of the brain and spinal cord differ in respect to their form, size, number of processes, shape, and number of their nuclei, etc., so a different physiognomy is presented by those of different parts of the sympathetic system.

Form.—The most common forms presented by the sympathetic nerve cells are oval, round, pear-shaped, or fusiform. Bidder has described cells from the cæliac ganglion with rectangular borders, which appear like cubes arranged in longitudinal rows. I have frequently met with similarly formed cells in the sympathetic of the Frog.

Size.—In any cluster of ganglion cells collected into a ganglion, the cells are found to exhibit extraordinary differences in their size, so that one cell may be four times as large as another with which it is in contact. It was formerly admitted

Fig. 262.

Fig. 262. Three quadrate and linearly arranged cells.

on insufficient evidence, that the sympathetic nerve cells were, on the average, of smaller size than those of the nerve centres; the incorrectness of this statement may, however, readily be demonstrated, as there is no difficulty in isolating cells of the largest calibre from the sympathetic ganglia. The cells appear to be of semi-solid consistence, but to possess a certain amount of elasticity, since after their form has been altered by pressure or other mechanical agency, they immediately resume their original shape on its removal.

With our present means of examination we are able to distinguish, in the sympathetic nerve cells, a *sheath*, a *proper*

cell-substance, a *nucleus*, and a *nucleolus*. The *sheath* or *capsule* of the ganglion cells cannot be considered in the light of a cell-membrane, but is rather the analogue of the sheath of the nerves; it consists of connective tissue, in which numerous nuclei are distributed. The relation of these cell-capsules to the connective-tissue sheath of the ganglion has been already referred to. Frantzel has demonstrated the presence of a single layer of polygonal flattened cells on the inner surface of the capsules, both in Man and other animals. They sometimes exhibit concentric striation with interspersed nuclei.

Beale and Remak explained all these peculiarities, which essentially result from the encapsulation of the cells by connective tissue, as due to nerve fibres. J. Arnold has endeavoured to show that a double investment exists in the nerve cells of the Frog, one proceeding from the perineurium of the nerve trunk, and the other from the neurilemma of the afferent nerve fibre. In prepared specimens, as the result of manipulation, the cells may often be seen perfectly naked, and without any trace of a connective-tissue sheath.

The *body* or *substance* of the nerve cells consists of a homogeneous matrix, in which numerous fine molecules are distributed. Arnold and Bidder have not been able to observe clearly the fibrillar structure described by Max Schultze, as presented by the ganglion cells.

A moderate number of fine fibres radiating from the nucleus and nucleolus may not unfrequently be seen running through the cell substance. These fibres, of the existence of which I, with Arnold and others, have convinced myself, form, according to Arnold and Courvoisier, plexuses. The existence of such a plexus resulting from the intercommunication of fibres running in the substance of the nerve cells has, however, been disputed by many observers. Kölliker only admits the existence of a plexus on the surface of the cell, which he believes belongs exclusively to the capsule. But, like Arnold, I have observed that these filaments occur in cells that have been detached from their sheaths. Sander ascribes these plexuses to fissures of the cell substance, a view that obviously originates in the examination of carelessly prepared cells. Frantzel believes that

the appearance of a fibre plexus may proceed from the lines of junction of the polygonal epithelial cells situated upon the inner surface of the capsule.

The sympathetic nerve cells, especially in Man, contain pigment of yellow or reddish-brown colour, which is usually of granular character, and is either distributed through the whole substance of the cell, or is accumulated at one spot. The microchemical peculiarities of this pigment have not been hitherto minutely examined.

The *nucleus* of the sympathetic cells is large, with a well-defined outline, which is peculiarly distinct in specimens prepared with chloride of gold, when the whole nucleus appears light, in relief against the violet-coloured cell substance. By some the existence of a special membrane is admitted around the nucleus, a deduction that has been made from the very distinct double contour line surrounding it, which appears after the action of various reagents. J. Arnold contested the

Fig. 263.

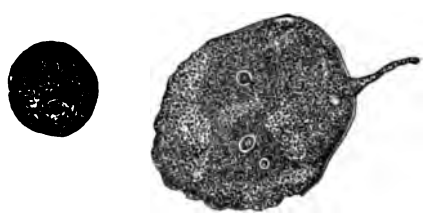

Fig. 263. Cells with two nuclei, one from the Rabbit, the other from the Frog.

existence of a special membrane in the nucleus, and I have not been more successful than he in satisfying myself from my numerous observations on sympathetic nerve cells, and still less on isolated nuclei, of the presence of a special membrane to the nucleus. The substance of the nucleus is not homogeneous, but is traversed by fine filaments which proceed from the nucleolus.

Remak long ago made a statement that has been more recently corroborated by Guye, Schwalbe, and others, to the effect that the greater number of the cells in the sympathetic

of the Rabbit and of the Guinea-Pig possess a double nucleus, an observation, of the correctness of which we may satisfy ourselves by the simplest preparation of a sympathetic ganglion from a Rabbit. I have myself on many occasions observed the presence of two nuclei in the sympathetic nerve cells of the Cat and Dog, and of Man. Bidder admits the presence of a communication between the two nuclei of the double nucleated cells, which is established by a fine thread or filament, and I can thoroughly corroborate his statement from my own observation. In nuclei that had been isolated from the cell substance I have likewise found these "nucleus connecting fibres," so that it was impossible to mistake them for any folding of the sheath, coagulation in the substance of the nerve corpuscle, or the like.

The *position* of the nucleus is very variable, both in regard to the situation which it takes up in the matrix, and also in the relations of one nucleus to another when two are present. In some instances the nucleus is displaced towards the surface of the cell, so that it even causes it to project, whilst in other cases it occupies the centre. When the nuclei are two in number, they vary still more in their position, lying sometimes nearly in the same plane, and at others being situated in various planes beside or subjacent to one another, separated sharply from each other by cell substance. Those cases in which the nuclei lie in nearly the same plane are exceedingly well adapted to show the above-mentioned fibres of communication between the nuclei.

Like the cells themselves, the nuclei also exhibit no inconsiderable differences in regard to their *size*. In researches made upon the nerve corpuscles from the ganglia of various animals, this relation is not to be overlooked. Thus we find, in scrutinizing the everywhere abundant nerve cells in the nerve plexuses accompanying the large vessels of the abdomen in the Frog, sometimes large cells with only one big nucleus; sometimes large cells with a single big and many small nuclei (polar nuclei, Courvoisier); thirdly, large cells filled with a number of small nuclei; fourthly, small cells, the interior of which is almost entirely occupied by the nucleus, the investing zone of cell substance being very thin; and, lastly, cells in which a

number of small nuclei are surrounded by a small quantity only of cell substance. Similar varieties of form may be observed also in Mammals, as in the Rabbit, Dog, and Cat, though particular forms appear to predominate in each. I intend to revert with greater detail to the significance of the relations just described.

The *nucleolus* is a structure that nerve cells usually exhibit with extraordinary sharpness of outline. It is, however, peculiarly distinct in the strongly pigmented cells of the adult Man, where it shines out from the cloudy substance of the cell and of the nucleus. Its position in the nucleus varies just as that of the nucleus within the cell differs in different instances, and, like this, the nucleolus is not unfrequently double or multiple, the several nucleoli in the latter case presenting at the same time a similar or varying magnitude. In the nucleolus

Fig. 264.

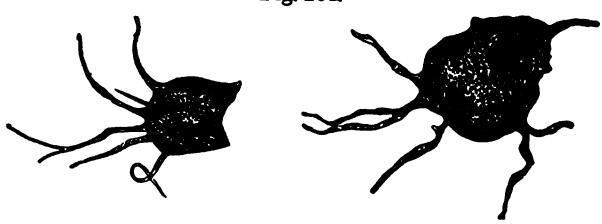

Fig. 264. Two multipolar cells, one from a child, the other from an adult.

itself a still smaller molecule may occasionally be observed (Beale), the existence of which was originally noticed by Mauthner in the cells of the spinal cord. Svierczewski described movements in the nucleolus similar to the molecular movements, which lasted for a considerable period if the preparation were protected from desiccation.

The presence of processes constitutes an important characteristic of the sympathetic, as of the nerve cells of the central organs of the nervous system. It was formerly maintained by many observers that apolar cells, or cells destitute of processes, occur in considerable numbers in the sympathetic; but at present the greater number of microscopists consider the existence of apolar cells to be doubtful. It is certain that the

older inquirers were too much inclined, from seeing cells without processes before their eyes, to draw the conclusion that, however common, the emission of processes was not constant in all ganglion cells. But inasmuch as the processes very easily tear away from the cells in the manipulation requisite to exhibit them, whilst, on the other hand, the larger size of the cells renders their discovery difficult, the conclusion is perhaps justifiable, that in a very large number of cases the supposed absence of processes is due only to the fact that they have been artificially detached.

Nevertheless I must still maintain with Kölliker, that cells occur in the sympathetic, in which no trace of processes is to be discovered, nor any indications of their having been torn away.

Moreover, the formerly mentioned cubical cells arranged in longitudinal rows defeat every effort to demonstrate processes in them, as Bidder has recently pointed out. It would appear, however, that these apolar cells are in process of development, and have not commenced to discharge their proper functions.

Fig. 265.

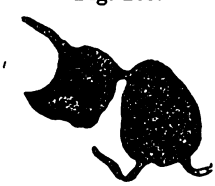

Fig. 265. Two cells united by a short bridge.

The greater number of the sympathetic ganglion cells are undoubtedly multipolar; the processes they give off run in part into nerve fibres, whilst others simply serve to bring two ganglion cells into communication with each other. In the latter case the processes are usually very short, the anastomosis appearing as a short bridge passing between the cells. Such a connection, however, is but rarely seen, probably in consequence of the injury done to the parts in the act of preparation.

A division of the processes into the categories established by Deiters, of axis-cylinder processes and ramifying processes, has

also been attempted to be maintained. Schwalbe describes a case in which an isolated cell from the sympathetic of the Cat exhibited such a division of its processes into several branched processes and a single cylinder axis. Bidder also mentions having seen similar instances. I have myself isolated a cell from the cæliac ganglion of the Rabbit, which, besides possessing several branched processes, also exhibited very distinctly two other processes which, at a short distance from the cell, became invested with nerve medulla, and were consequently to be regarded as axis-cylinder processes. From this it would appear that the axis-cylinder process is not always single. Auerbach has called attention to a peculiar arrangement of unipolar cells, which he has named "opposed" or "twin" cells ('opposite Stellung der Zellen'). Here two cells are contained in a single sheath, and each gives off a single process in opposite directions from the poles which are averted from each other. Like Schweigger-Seidel, I have not unfrequently met with this form in various parts of the sympathetic.

Fig. 266.

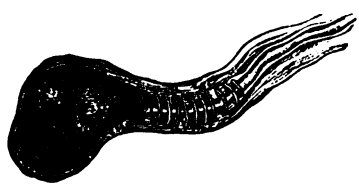

Fig. 266. Ganglion cell, with spiral fibre.

An important advance in the path of discovery in regard to the nature of the processes of the sympathetic nerve cells was made by the simultaneous discovery of L. Beale and J. Arnold, that two processes are given off from the small end of the more or less bell-shaped nerve cells in the sympathetic of the Frog. One of these pursues a straight course, the "straight fibre" of both authors, whilst the other forms a series of coils around this, and constitutes their "spiral fibre." Both the straight and the spiral fibre lie within a common and usually nucleated sheath, which represents the direct continuation of the sheath of the ganglion cell. Nucleated enlargements not unfrequently

occur in both fibres, similar to those that have been so often described as exhibited by non-medullated nerve fibres. After running in company for a variable distance, the two fibres separate from one another, and pursue an opposite course. Both are essentially nervous, as is clearly shown by the circumstance that Arnold and Beale have been able to trace the continuity of both processes with dark-edged motor fibres.

The relation of the spiral to the straight fibre is subject to great variation, both in reference to its thickness and to the number of its coils. As a rule, the straight is thicker than the spiral fibre, though the difference is sometimes not very well marked, and is occasionally the reverse. The spiral fibre is frequently multiple, and is then usually of smaller size than when solitary. The number of coils is likewise very variable, and in some instances the spiral character or type is not apparent, the two fibres then running parallel to one another, whilst in other cases the spiral fibre is wound round the straight like a corkscrew. According to Beale, it is in young cells that the spiral fibre is defective, whilst, on the contrary, the older the cell, the greater the number of the coils. In my investigations undertaken with this particular point in view, I have convinced myself that the spiral fibre, though undoubtedly very common, is not uniformly present in the sympathetic cells of the Frog. Great differences exist in this respect in different individuals, rendering it very probable that they stand in relation with the various stages of development through which the nerve cells pass.

Arnstein and Kollmann, Courvoisier, Guye, and Bidder, all essentially adopt the views of Arnold and Beale in regarding both of the processes springing from the sympathetic cells as nervous structures. Schwalbe is inclined to admit two kinds of spiral fibres, one of a nervous nature, originating in the substance of the ganglion cell, and making only a few or no turns around the straight fibre; the other, which may be regarded as produced by a thickening of the sheath, and as being developed from a fibrous plexus at the base of the cell. Krause held the spiral fibres as unessential structures, which were not of a nervous nature, and believed that they either consisted of an elastic fibre, or were referable to the foldings of the

neurilemma. Sander has substituted for this explanation the view that the spiral fibre is to be regarded as due to the fissures and foldings of the inner sheath of the straight fibre. These observers have been as unsuccessful as Kölliker in following the spiral fibre into a dark-edged nerve fibre.

The spiral fibre, the existence of which was first ascertained in the sympathetic cells of the frog, occurs also in the higher Vertebrata; in the latter, however, the spiral coils are less distinctly marked, and the course of the two processes from the same pole of the cell is more or less parallel.

Since the discovery of the spiral fibre, some confusion has arisen in the nomenclature of these cells, owing to the circumstance that some authors, as Arnold and Guye, name those from one pole of which two processes are given off, unipolar cells, whilst others, as Beale, Kollmann, and Arnstein, term them bipolar. Courvoisier proposes to name the point where the straight and the spiral fibre are given off the holopole, twin pole, or simply the pole; each separate cell might then be considered to have a hemipole for its origin. Cells with two fibres springing from the same point Courvoisier desires to be named geminipole cells.

As regards the place of the origin of the processes, histologists are divided into two sets, as has been already explained in Chapter III. Some, as Arnold, Frántzel, Arnstein, and Kollmann, and, to some extent, also Bidder, besides the older authors, refer the origin of the fibres to the nucleus and the nucleolus of the cells; whilst others, as Kölliker and Schwalbe, deny the existence of any intimate connection between the processes and the nucleus and nucleolus; Courvoisier admits that though he has traced the straight fibre to the nucleus, he has not seen it terminate either in it or in the nucleolus.

In the very great number of cells that I have investigated in reference to this point, especially amongst those that have been taken from the sympathetic of Mammals, I have always observed that the processes originate in a direct prolongation of the cell substance into the process, and I have never perceived any connection between the cell process and the nucleus or nucleolus. We sometimes see, as Schwalbe has stated, that the process breaks up into a divergent brush of filaments at the

point where it enters the cell. But I have also satisfied myself that very frequently, besides the relatively thick processes that originate in the cell substance itself, a second system of very fine filaments is given off, that take their origin from the nucleus and nucleolus. These fine processes are nothing else than the already mentioned nuclear and nucleolar filaments. They run in part in the track of the coarse processes, and in part pursue their own path; it very seldom happens, however, that these fine fibres can be traced for any considerable distance after their emergence from the cell substance. On one occasion I observed a fine process of the kind just described become continuous with the axis-cylinder of a medullated fibre; and Beale has made a similar observation. The origin of the straight fibre from the nucleolus, which is now and then observable, cannot certainly be regarded as the rule. In fig. 267 a cell from the sympathetic of the Frog is depicted, where the straight process, in which with high powers a fibrillar structure may be established, penetrates through the cell substance to the nucleus. After having been traced to this body, however, its precise mode of ending escapes observation. Nevertheless, I do not doubt but that, under favourable circumstances, the straight fibre could in some cases be shown to be directly continuous with the nucleolus.

Fig. 267.

Fig. 267. Exhibiting the nerve process extending as far as to the nucleus.

Further, the various authors are not agreed upon the point of origin of the spiral fibre. Arnold has stated that it develops from a plexus formed by the nucleolar filaments in the substance of the cell. Beale considers that it proceeds from the more superficial portion of the cell substance, where a few accessory nuclei usually lie. The view of Arnold received in the first instance the most complete corroboration by Courvoisier, but in a later publication he has admitted it with some

reserve. He describes in addition connecting fibres proceeding from the nucleolar fibrous plexus to adjoining ganglionic cells, to which he has applied the name of commissural fibres. Arnstein and Kollmann observed fibres which converged from the deeper parts of the cell substance towards the peduncle of the cell, from the plexiform union of which they considered the spiral fibre to arise; but they were unable to establish the connection of this plexus with the nucleolar filaments. Bidder was unable to satisfy himself of the continuity of the fibrous plexus, the existence of which he allows, with the spiral fibre.

As regards the physiological significance of these two processes, we can only form presumptions at present. Arnold regards the straight fibre as the afferent (proceeding from the cerebro-spinal organs) and the spiral as the efferent (running towards the periphery). Arnstein and Kollmann take the same view. According to the researches of Courvoisier, in which he studied the degenerative processes appearing after division of the rami communicantes, the straight fibres first degenerate, then the cells, and lastly the spiral fibres. These results are in favour of Arnold's view. On the other hand, Bidder also, relying upon the results of division of the vagus of the Frog, regards the spiral fibres as the afferent and the straight fibres as the efferent fibres.

Beale has supplied a large amount of information upon the continuous processes of development and degeneration taking place in growing and adult individuals. His most important arguments rest on the coincident presence in the sympathetic of the same individual, of cells of the most various size, form, number, and nature. Beale admits three types or modes of development of nerve cells.

In the first of these the cells arise in a finely granular mass resembling that in which the embryonal tissues are developed, with which nerve fibres are in connection; in the second new cells arise by division of a nerve cell; and in the third the cells develop from the nuclei of nerve fibres. The observations and deductions of Beale have received little attention in Germany. Sander has opposed the statements of Beale; though, as far as my experience goes, incorrectly. The various forms of ganglion cells described by Beale, which appear to correspond to various

stages of development, may be observed, though certainly not with equal frequency in all individuals, in the Frog. Moreover, in the ganglia of the Mammals I have investigated, there are evidences enough to show that active processes of development are taking place in them, as, for example, the extraordinarily various size of the nerve corpuscles and of the nuclei, the presence of diffuse, finely granular masses with numerous dispersed lustrous corpuscles, the serially arranged cells without processes, etc. I intend to discuss these points in more detail elsewhere. In investigations made upon the sympathetic of the Frog, the attention of the observer is especially attracted to clusters of small corpuscles composed of nuclei, with small surrounding area of protoplasm, invested by a capsule of connective tissue. These cell clusters are aggregated together in variable numbers, and are again enclosed in a common capsule composed of connective tissue, which is in many instances nucleated. The formations just described stand in connection with nerve trunks, and are met with in very variable numbers in different individuals.

Fig. 268.

Fig. 268. Cell-cluster.

The fibres of the sympathetic proceed in part from the cerebro-spinal organ, and partly arise from the sympathetic nerve cells. In the rami communicantes, fibres run both from the spinal cord and the spinal ganglia towards the sympathetic system, and also in the inverse direction. These last fibres may either continue their course in the spinal cord, further towards the centre, or may join the tract of spinal nerves, and run towards the periphery of the body. According to Courvoisier, in the animals he examined, including the Pigeon, Rabbit, and Frog, the rami communicantes spread themselves in equal proportions both upwards and downwards in the principal

trunk of the sympathetic, while in the spinal nerves about one-third run towards the centre, and about two-thirds towards the periphery. The fibres proceeding from the cerebro-spinal organs run, not only through the sympathetic ganglia, but they are also continuous with its cells, as Courvoisier has again recently demonstrated by researches made upon sections of the rami communicantes, with subsequent examination of the resulting degenerative processes. On section of the rami communicantes the greater part of the fibres of the sympathetic portion of the trunk undergoes degeneration; and the cells also participate in the processes of degeneration in a peculiar mode that has been described by Courvoisier. The spinal segment of the section degenerates only in small part. According to Courvoisier, the degeneration in the fibres of the sympathetic stump of the rami communicantes is primary and tertiary; that is to say, in the latter case, after attacking the cells, is transferred to the fibres proceeding from the cells. As regards the nature of the fibres of the sympathetic, the view that the sympathetic nervous system is characterized by the occurrence of medullated fibres of much finer calibre than those of the cerebro-spinal system, is now given up. It is undoubtedly true that fine dark-edged fibres of medium size are abundantly and widely distributed, as well as the various kinds of non-medullated fibres. In regard to the character of these structures, the reader is referred to the third chapter of this work. The so-called transitional fibres of Courvoisier, which alternately cast off and resume their medullary sheath, I have not unfrequently seen in the sympathetic of the Frog. Whether these fibres are to be regarded as artificial products, as some authors maintain, can only be determined by further investigation.

As regards the mode in which the fibres of the sympathetic nervous system are distributed, their rough anatomy, the course and relation of the principal trunk, the number of ganglia, etc., will be found described in manuals of systematic anatomy. Dating from the excellent researches of Remak and Bidder, sympathetic ganglion cells have been discovered in great numbers in almost every organ of vegetative and generative life.

In the *apparatus of circulation*, the heart contains ganglion

cells (Remak and Bidder; see also chapter VII. of this manual), as do also the vessels (Beale, Lehmann), and the sympathetic glands (Schaffner). Luschka has described ganglion cells in the *coccygeal gland*, which, according to the most recent investigations, must be regarded as an appendage of the vascular system; this statement, however, has not been corroborated by other observers. In the *digestive tract*, ganglion cells have been found by Remak and Meissner, in the submucous layer throughout its whole length, from the pharynx downwards, and in the muscular layer by Auerbach; very recently Trütschel has described a layer of large multipolar cells lying upon the muscularis mucosa of the mucous membrane of the stomach. These cells are of a nervous nature, and are connected together by processes. Ganglion cells have been found in large numbers by Krause and Schlüter in the salivary glands (oral glands and pancreas) associated with the digestive apparatus. Ganglion cells have also been described by Manz in the excretory ducts of the liver and pancreas.

In the *respiratory apparatus*, nerve corpuscles have been discovered in the lungs, and in the tissues of the larynx and trachea. The *urino-genital* apparatus contains ganglion cells distributed through the bladder and ureters, the testes (Letzerich), the prostate and erectile tissue of the penis (Lovén), the vas deferens, vagina, and uterus. Ganglion cells have also been found in some of the so-called *ductless glands*, as in the adrenals, and recently by Fleischel in an organ which he considers to be the thymus of the Frog. Similar cells have been found by H. Müller, in the *lachrymal glands* connected with the eye, and in the *ciliary muscle*. In the *iris* of the Fowl, which consists of striated muscular tissue, v. Hüttenbrenner has observed cells which he is inclined to consider nerve cells. More detailed accounts of the peripheric ganglion cells distributed through the several organs mentioned above, may be found under their special headings.

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The reader is referred for the older literature of this subject to several of the treatises cited, and to Kölliker's "Handbook."

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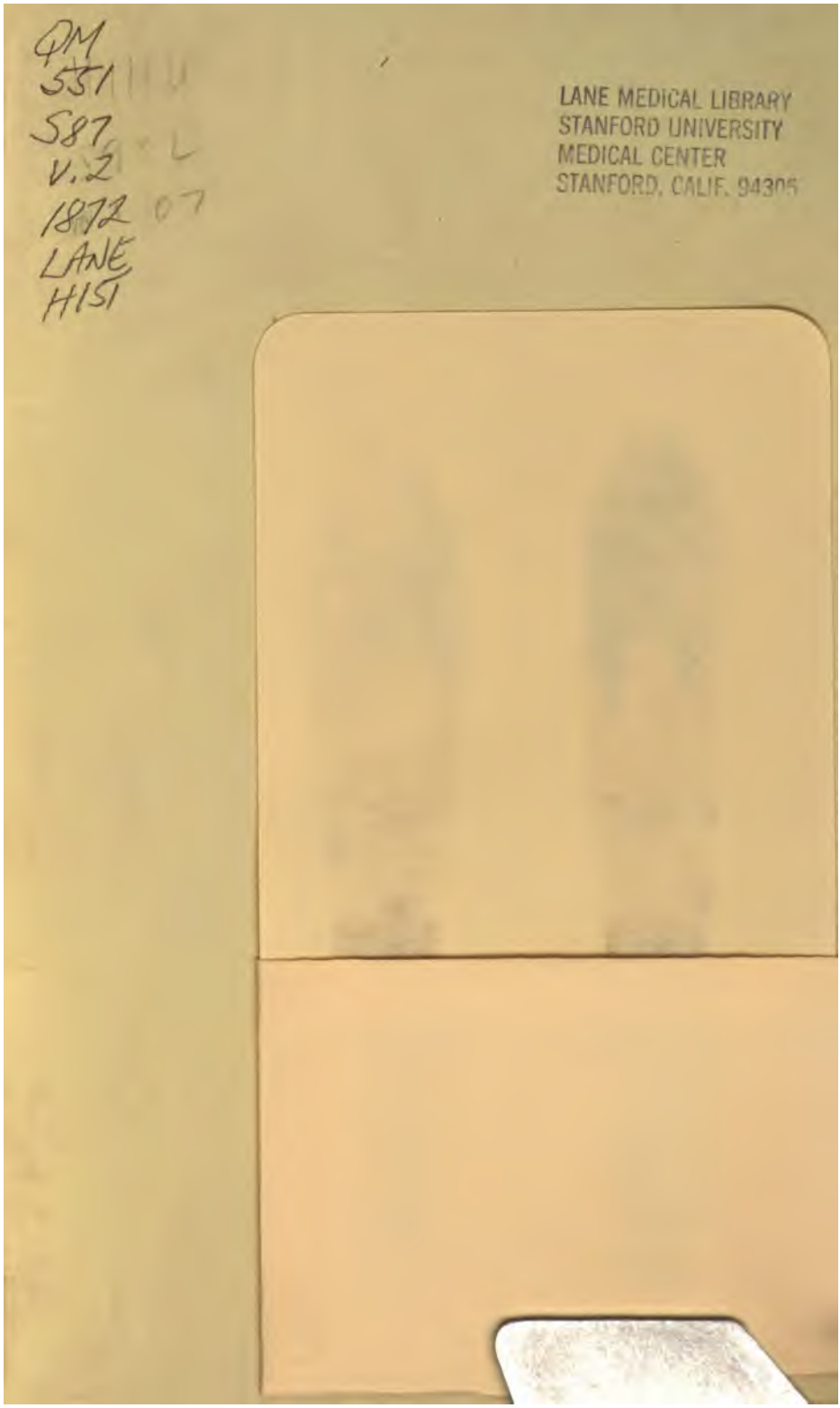
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